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Development of Various Quantitative and Analytical Methods for the Analysis of the Dynamics of Fish Populations: An Application to the Spotted Seatrout Population in Coastal Louisiana.

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DEVELOPMENT OF VARIOUS QUANTITATIVE AND ANALYTICAL METHODS FOR THE ANALYSIS OF THE DYNAMICS OF FISH POPULATIONS: AN APPLICATION TO THE SPOTTED SEATROUT POPULATION IN COASTAL LOUISIANA

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF SYMBOLS

C_t - Catch of fish at time t.

E_t - The proportion of fish alive at the beginning of time t that are subsequently captured.

F_i - the instantaneous fishing mortality in the ith iteration step.

l_j - mean size of fish in size-class j.

l_o - mean size of fish caught in mesh size i

m_i - size of mesh i, specifically stretch measure in inches.

M_i - Instantaneous rate of natural mortality in the ith interval.

n_i - Summation of fish of size-class j in mesh size i, i.e. n_{ij}.

N_i - Surviving number of fish at the beginning of the ith interval (e.g. $N_i=N_0*\exp(-(M_i+F_i))$.

n_{ij} - catches of fish of size-class j in mesh i.

N_j - relative number of fish of size-class j in the population.

p_{ij} - relative frequency of fish of size-class j in mesh i, i.e. $n_{ij}/\Sigma_i n_{ij}$.

q_i - skewness coefficient of the catches of fish size-class j in mesh i.

Q_i - V_{t+1}/C_t*E_{t+1}, which is the constant in the integration of Baronov's catch equation.

s_{ij} - selectivity of mesh m_i to fish of size-class l_j.

S_{ij} - standardized selectivity or probability of capture, i.e. $s_{ij}/max_i(s_{ij})$.

U_i - $F_t*(1-e^{-Zt})/Z_t$, the exploitation rate in the ith iteration step.

V_t = The "virtual population" at time t, or the number of fish "destined" to be caught over the remainder of the life of the year-class.

Z_i = the total instantaneous mortality in the ith iteration step.

σ_i = standard deviation of the catches of fish size-class j in mesh i.

ABSTRACT

Presented in this dissertation are analytical and quantitative methods developed for an experimental gillnet sampling program for the analysis of the dynamics of fish populations, which are illustrated here on Louisiana's highly prized spotted seatrout population.

Chapter 1 presents a new method of estimating gillnet selectivity using a system of simultaneous equations and a non-linear iterative maximum likelihood approach. The model solution is a set of parameter estimates which mathematically describe the response surface of capture probabilities for fish of size-class j in mesh size i.

As an extension to the nonlinear maximum likelihood gillnet selectivity model, Chapter 2 presents a second approach which uses the probability of capture to estimate the relative abundances of the various size-classes of fish in the population and develops a variance estimator for the relative abundances. The selectivity model and variance estimation procedures were applied to the experimental gillnet catches of spotted seatrout from 1988 to 1990.

In Chapter 3, several multivariate statistical techniques were applied to the experimental gillnet catches of spotted seatrout to examine the distributional ecology of the population. Principal Components Analysis (PCA) revealed a two factor model which explained 78% of the variation in the covariance matrix of the original data. The Principal Component factor loadings were interpreted as recruit (juvenile) and spawner (Adult) abundance for factor 1 and factor 2, respectively. Linear regression analysis showed recruit and spawner

abundance had a high positive correlation to salinity during the spawning season, but slopes between the two life history stages of seatrout varied significantly ($p<0.05$). After the spawning season (September-December) recruit abundance showed a high negative correlation to salinity. Implications of the non-uniform spatiotemporal distributions of spotted seatrout abundance to management are discussed.

Finally, in Chapter 4, a population level assessment is conducted on the spotted seatrout fishery in Louisiana to estimate fishing mortality at age, population size at age, and spawning potential ratios using a Monte Carlo-based Virtual Population Analysis (VPA). Application of the Monte Carlo based simulation (N=3000) was used to characterize uncertainty in the VPA model output of spawning potential ratios which arise from uncertainty associated with input parameters of natural and terminal fishing mortality.

INTRODUCTION

The populations of estuarine and marine finfish in Louisiana's coastal waters support economically valuable recreational and commercial fisheries (Titre et al. 1988). Louisiana's spotted seatrout and red drum resources, in particular, have received national interest (Treen 1983, GTSFM 1984). Increases in fishing pressure on and conflicts between fishing interests over these stocks in the 1970's and 1980's resulted in the creation of the Governor's Task Force on Saltwater Finfish Management (GTSFM 1984). In fulfilling its charge, the GTSFM suggested the objectives for management and made other relevant recommendations addressing the protection of the finfish resources.

The GTSFM's management objectives for Louisiana's valuable fishery resources were to be based on sustained optimum yields and the biological conservation of the fish stocks (GTSFM 1984). In order to achieved management objectives such as these, suitable data have to be made available and of adequate statistical quality to give answers of required precision. Two main sources of data needed are: those obtained from sampling the commercial and recreational fishery which provide information about the effects that the fishery has on the stocks of fish; and those collected from a fishery-independent sampling program which provide needed additional information on abundance and recruitment (Pope 1988).

Therefore, one of the GTSFM's major recommendations was that a saltwater finfish research unit be established within the Louisiana Department of Wildlife and Fisheries (LDWF) and that this unit be

charged with implementing a coast-wide stock assessment program focusing on spotted seatrout and red drum populations (GTSFM 1984). The LDWF responded to this charge through the creation and implementation of a coast-wide fishery-independent finfish monitoring program in 1985 whose objective was to provide information on the population dynamics of the finfish stocks.

The abundance of fish in a population, and thus the harvestable biomass to a given fishery, depends upon the stocks dynamics which is affected by processes in recruitment, growth, and mortality (Ricker 1975). Therefore, accurate estimates of fish abundance are fundamental to fisheries management (Rounsefell 1975; Kjelson and Colby 1977) and the estimation of recruitment is essential to understanding the stocks dynamics (Ricker 1975, Cushing 1977, Gulland 1977).

Standardized fishery-independent sampling programs, such as that implemented in Louisiana, are needed to estimate the vital rates of fish populations, including mortality and recruitment, and to provide indices of stock abundance (Gulland 1985). Further, fishery-dependent catch statistics, upon which most population assessment models are based, are almost always biased and will need to be augmented by a standardized sampling program (Pope 1988). Therefore, a healthy fisheries program is likely to combine elements of both (Pope 1988).

This study was initiated in cooperation with the LDWF to develop analytical and quantitative methods which can be applied to the catch data from the finfish monitoring program to provide standardized indices of abundance for the assessment of the spotted seatrout fishery. The quantitative methods presented in this dissertation were developed

specifically: 1) to minimize sources of bias in the catch data (which is not possible with catch data alone) using an analytical approach to estimate the selectivity of the gear; 2) to produce consistent year to year indices of stock abundance and develop a method of estimating variances of those indices; 3) to examine changes in the stocks distribution patterns (catchability) brought about by variable environmental patterns; and 4) to provide a method of examining the sensitivity of assessment model output which arise from input parameter uncertainty. These methods, while applicable to any fish species that is effectively sampled by the experimental gillnets, is illustrated here on Louisiana's highly prized spotted seatrout population.

As is true of most gears used to sample fish populations, experimental gillnets do not capture all fish exposed to them with equal efficiency (Richkus 1980). For each species of concern, it is necessary to estimate the selectivity (efficiency) of the various mesh sizes in the experimental gillnet for the different size-classes of fish in the population, with which accurate estimates of abundance can be obtained (Kjelson and Colby 1977). Chapter 1 of this dissertation is devoted to the estimation of the selectivity (or fishing efficiency) of each mesh size used in the multi-panel experimental gillnet for the various size-classes of spotted seatrout in the population from which the sample was drawn. The analytical technique developed here provides quantitative estimates of mesh selectivity which minimize biases associated with estimates of abundance of the various size-classes of fish in the population.

Application of this technique to the fishery-independent sampling program enables consistency in the estimation procedures from year to year, thus avoiding other sources of bias, which is not possible with fishery-dependent data (Pope 1988). However, it is also important to assess the level of certainty one can place in the abundance estimates by examining their variances. Chapter 2 extends the utility of the gillnet selectivity modeling approach, developed in Chapter 1, one step further by estimating the variances associated with annual estimates of the relative abundances for spotted seatrout from 1988 to 1990. The quantitative methods developed in these first two chapters provide a tool for understanding the population dynamics of a fish stock, particularly in terms of recruitment and mortality.

The process of capturing fish is intrinsically related to fish abundance and their distributions, both in time and space, which are often driven by changes in the environment (Csirke 1988). Catchability is a quantitative description of the capture process which expresses the fraction of the stock captured by one unit operation of fishing (Ricker 1975). Assessment models and effective management of the stock often suffer from a lack of knowledge concerning changes in the catchability of fish, whether through changes in gear efficiency or by changes in behavior brought about by environmental factors. Therefore, knowledge of the stocks spatial and temporal distribution patterns as well as the environmental forces driving those patterns is essential to manage the fishery. Chapter 3 of this dissertation develops a quantitative approach for determining the distributions of fish abundance. A multivariate statistical approach is applied to the experimental gillnet

catch data of spotted seatrout to discern the distributions of fish abundance over spatial and temporal scales. This approach statistically identifies likely important environmental factors and tests whether the distribution patterns are dependent on a specific life history stage of fish in the population.

Management advice is often based on the results of assessment models, many of which are by nature deterministic, that is a given set of estimated input parameters (used without a measure of their intrinsic uncertainty) results in only one output solution. Without techniques to characterize the sensitivity in assessment model output, managers can not give adequate advice relevant to the risks involved in setting incorrect biological references points. Little work has been done to characterize model output sensitivity which results from the uncertainty associated with model input parameters. Pope (1988) among others has suggested simulation studies involving the Monte Carlo technique as a useful approach to assess model sensitivity (Pope 1988). Chapter 4 of this dissertation applies a Monte Carlo-based simulation to an assessment model which is currently proposed as the basis to manage the spotted seatrout fishery resource in the State of Louisiana. The intent of this study is to provide managers with a quantitative method to appraise the sensitivity of assessment model output which results from input parameter uncertainty.

Primary Data Set and Assumptions

The primary methods developed in this dissertation, the first three chapters, are based upon the experimental gillnet catch data from the Louisiana Department of Wildlife and Fisheries' Finfish Monitoring Program. Biological, hydrological, and environmental data have been collected as part of Louisiana's finfish monitoring program since 1985, when this program was initiated. The gears used in this monitoring program include beach seines, trammel nets, and multi-panel experimental gillnets and are intended to sample the juvenile, sub-adult, and adult life history stages of many important estuarine and marine populations of finfish. The multi-panel experimental gillnets have been proven as an effectively means of capturing various sizes of adult and sub-adult spotted seatrout in coastal Louisiana (Adkins and Bourgeois 1982).

Stations selected for this sampling program were positioned roughly along transects extending from the lower salinity, brackish marshes to the higher salinity, lower bays and beaches of Louisiana's coastal zone and are intended to cover some of the various finfish habitat and salinity regimes typical of the estuaries in Louisiana. Each station was sampled twice monthly for physical variables such as temperature, salinity, turbidity, and tidal stage. Biological variables include the catches of finfish in the various gears deployed, and specifically by mesh size for the experimental gillnets. With the experimental gillnets, biologists employed a "run around or beat down" method to capture fish in monofilament nylon experimental gillnets which were comprised of five different mesh sizes: 2.0, 2.5, 3.0, 3.5, and 4.0

inch (5.08, 6.35, 7.62, 8.89, and 10.6 cm, respectively) stretch measure. At each station, the experimental gillnets, measuring 750 ft (228.6 m) in length (150 ft per mesh panel), were deployed by biologists and encircled three times by the fishing vessels to drive fish into the nets. The nets were then retrieved, starting with the panel first entering the water, and the catch enumerated by mesh. Specific biological information was collected for spotted seatrout which included length, weight, sex, maturity state, and gut content.

The quantitative and analytical methods developed in this dissertation (Chapters 1 through 3) are specifically applied to the multi-panel experimental gillnet catch data between 1988 and 1990. These methods provide a quantitative tool useful for the analysis of the dynamics of any fish population for which the underlying assumptions apply, but are illustrated in this dissertation for spotted seatrout.

As with any method or model which analyzes fish populations, certain assumptions must be made so that reasonable inferences regarding the sampled population can be extended to the population of interest. Two primary underlying assumptions are made with regard to the spotted seatrout population being sampled. First, it is assumed that the population of interest about which inferences are to be made is restricted to the inshore waters of the coastal zone (since stations do not extend much beyond the barrier islands), and that emigration of fish out of the sampled area is minimal. Second, it is assumed that gear

avoidance is not size related and that, within the population sampled, all sizes of fish have an equal probability of encountering the gear.

The second assumption is very difficult to verify with the data used in this analysis and direct studies are needed to specifically address this problem. The limited data do, however, support the first assumption. Published studies on spotted seatrout movement or migration out of the inshore waters suggest adults are relatively non-migratory and that their movements are restricted to a particular estuary (Iverson and Tabb 1962, Arnoldi 1984, Mercer 1984). Further, environmental factors, which have been suggested to be responsible for changes in the distribution patterns and gradual movements of spotted seatrout to the offshore waters (Mercer 1984), are only periodic and do not preclude the sampling of the general population over the course of the entire year.

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CHAPTER I

A New Method of Estimating Gillnet Selectivity, With an Example For Spotted Seatrout, *Cynoscion nebulosus*.[1]

Abstract

This study proposes a new method of estimating the selectivity of gill nets. Using data on the distribution of fish lengths from the catches of various meshes in an experimental gill net, a system of m equations and n unknown coefficients is simultaneously solved describing the functional relationship of the moments from an assumed mathematical model across mesh size and size-class of fish. The solution to the model is a response surface describing the probability of capture of fish of size-class j in mesh i. This new method is applied to spotted seatrout (*Cynoscion nebulosus*) in coastal Louisiana and used to estimate the relative abundance of the various size-classes of fish in the population. We suggest that this approach for estimating gillnet selectivity has several advantages over other methods: it is very flexible in terms of choosing a mathematical model which would best represent the data; it takes full advantage of the empirical data allowing catch information, n_{ij}, to contribute to the final solution both as a function of mesh size and size-class; and it offers

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simplicity and elegance in its overall iterative least squares approach and is tractable in terms of assessing the reliability of the parameters and model used.

Introduction

Experimental gill nets are often employed as fishery independent techniques for sampling fish populations and monitoring fish stocks. Experimental gill nets circumvent size selectivity biases encountered when using gill nets of a single mesh size, by fishing a series of different meshes (varying only slightly in size) simultaneously so that a broader range of size-classes in the population appear in the catch and the various size-classes of fish are represented in each of the meshes. Selectivity is the usual information obtained from gill net studies which can be used to estimate the relative abundance of the various size-classes of fish in the population (Olsen 1959; McCombie and Fry 1960; Gulland and Harding 1961) and is needed in managing a commercial gill net fishery (McCombie 1961; Jensen 1972; Ehrhardt and Die 1988).

Lagler (1968) defined the size selectivity of a gear to be the proportion of the total population of a certain size-class of fish which is caught and retained by a unit operation of fishing. Based on this definition, selectivity is the quantitative description of selection by a gear and is usually represented as the probability of capture of a certain size of fish in a certain sized mesh. If the true population size structure cannot be directly determined or accurately estimated then one must resort to indirect methods of estimating the selectivity

of the meshes. Most of the indirect methods which have been proposed in the literature follow one of two basic approaches: the use of "Type A" curves with methods developed by Olsen (1959), Holt (1963), and Hamley and Regier (1973); or methods which utilize type B curves as intermediaries such as that of Baranov (1948), McCombie and Fry (1960), and Regier and Robson (1966). Recently, another indirect iterative method has been proposed by Boy and Crivelli (1988) which requires an estimate of the population age structure. Regier and Robson (1966) define type A selectivity to represent the probability of capture of one mesh size to various size-classes of fish while type B selectivity gives the probability of capture of a single size-class of fish to different meshes. With suitable assumptions, various mathematical models have been used to estimate the shape of type A selectivity curves and Regier and Robson (1966) and Hamley (1975) provide a thorough review of these methods. We found the methods which use the "Type A" curve approach unsuitable for our data on spotted seatrout (Cynocion nebulosus) because of departures from the assumption of normality and/or incongruity between curves. Among those methods which use "Type B" curves, Regier and Robson (1966) found their computational approach better at estimating the selectivity of a 4.5 inch (11.4 cm) mesh for lake trout based on a known standard.

The model presented here arose out of an attempt to solve Regier and Robson's model by applying a non-linear iterative least squares approach to estimating the selectivities both as a function of mesh size and size-class of fish. The primary reasons for pursuing this different approach are twofold. First, it was felt that an iterative least

squares fitting procedure to the actual catches of fish of size j in mesh i might better describe the systematic change in Type A and Type B catch distributions simultaneously; i.e. fitting an overall response surface. Secondly, the approach would be tractable in terms of assessing the model's fit to the empirical data as well as the reliability of the parameter estimates.

We applied this new non-linear iterative least-squares fitting procedure to experimental gillnet catches of spotted seatrout and estimate the selectivity of the different meshes fished. The selectivities derived from the model are used to estimate the relative abundances of the various size-classes of fish in the seatrout population and the gillnet selection characteristics which are needed parameters to assess the status of the spotted seatrout stocks in coastal Louisiana.

Materials and Methods

This study is based on experimental gillnet data obtained from a coastal finfish monitoring program conducted by the Louisiana Department of Wildlife and Fisheries. State biologists employed a run-around method to capture spotted seatrout in monofilament nylon experimental gill nets in one of five possible mesh sizes: 2.0, 2.5, 3.0. 3.5 and 4.0 inch (5.08, 6.35, 7.62, 8.89, and 10.16 cm respectively) stretch measure. Fish tangled in the nets (768 fish), identified as those held in the net anterior to the gill covers or on body protrusions, were excluded and the 1988 gillnet catches of spotted seatrout used for

analysis. A brief description of fishing and data collection procedures will be provided here; however readers interested in specific methodology should consult Adkins and Bourgeois (1982).

Data were collected by teams of finfish biologists within seven hydrographic areas covering the entire coastal zone of Louisiana. Approximately eight to 14 stations within each zone were sampled twice monthly between January and October of 1988. At each station experimental gill nets, measuring 750 feet in length (150 feet per mesh panel), were deployed by biologists and encircled approximately three times by the fishing vessels to drive fish into the nets. The nets were then retrieved, starting with the panel first entering the water, and the catch enumerated by mesh. Fish were measured to the nearest millimeter, weighed to the nearest gram, and examined for stomach content and maturity stage.

List of Symbols

l_o = mean size of fish caught in m_i.

σ_i = standard deviation of the catches of fish size-class j in mesh i.

q_i = skewness coefficient of the catches of fish size-class j in mesh i.

l_j = mean size of fish in size-class j.

m_i = size of mesh i, specifically stretch measure in inches.

n_{ij} = catches of fish of size-class j in mesh i.

$n_i = \sum_j n_{ij}$.

N_j = relative number of fish of size-class j in the population.

p_{ij} - relative frequency of fish of size-class j in mesh i, i.e. $n_{ij}/\Sigma_i n_{ij}$.

s_{ij} - selectivity of mesh m_i to fish of size-class l_j.

S_{ij} - standard selectivity or probability of capture, i.e. $s_{ij}/\max_i(s_{ij})$.

Skew-normal probability density function:

$$s_{ij}=\frac{1}{\sigma\sqrt{(2\pi)}}\exp^{-(l_j-l_0)^2/2\sigma^2}x\left\{1-1/2q\sigma^{3/2}\left[\frac{(l_j-l_0)}{\sigma}-\frac{(l_j-l_0)^3}{3\sigma^3}\right]\right\} \qquad (1.1)$$

Model Development

Hamley (1975) stated that the shape of the type B selectivity curve can be estimated without bias by comparing the catches for fixed l_j across different m_i. Because the individual meshes themselves were fished with equal effort we assume that the probability of encounter of fish of a single size-class is equal with respect to the different meshes and that each mesh caught the same proportion of fish of the size-class for which that mesh is most efficient (equal catchabilities at the peak of each curve). Therefore, catches of a single size-class are proportional to the selectivities and s_{ij} can be determined by fitting a likely mathematical model on s_i for fixed l_j. This is referred to as type B selectivity (Regier and Robson 1966).

In addition to the probability of capture, we also use the term probability of occurrence to mean, on the average, the expected catch of fish of size-class j in mesh i given the size/age structure over the period of the study. Thus, the probability of occurrence of the various

size-classes of fish is a function of the population size structure and may change from one year to the next.

The probability of l_j occurring in m_i is roughly the proportion of fish caught of that size to n_i. The proportion across all size-classes in a given mesh resembles the size frequency distribution of mesh i and can be modeled using a variety of probability functions. Baronov (1948) envisioned the size distribution of catches from gill nets to look like a normal probability function as the mesh of a gill net would capture fish of a definite size and few whose length differed from the optimum by more than 20 percent. However, gillnet size frequency distributions are frequently either positively or negatively skewed and even multimodal.

For this particular data set we chose a skew-normal probability density function because of the pronounced skew associated with the distribution of catches from the meshes in our experimental gang. Regier and Robson (1966) used the skew-normal model to estimate the shape of type B selectivity curves, which they used as intermediaries to determine type A selectivity. This is essentially a normal probability function corrected for skewness using the first two terms of a Gram-Charlier series (Croxton and Cowden 1967). This is a three parameter function whose shape is determined by the mean (l_o), standard deviation (σ), and skewness (q). We wish to emphasize that the general procedure developed here can be used with other mathematical models, and one should be chosen which best describes the form of the data. Such models might include normal, log-normal, gamma, or the Weibull, particularly if a more flexible form is needed to fit the data.

Once an appropriate mathematical model has been selected, the approach is to solve simultaneously a system of m equations which describe the functional relationship of the moments of the catch distributions across m_i and l_j, using a non-linear iterative model which seeks a least-squares solution between the expected catch based on the model and the observed catch of fish. We propose the following method to solve this system:

Step 1. Calculate the moments of each distribution corresponding to the various mesh sizes fished. From our assumed probability function we would estimate l_o, σ, and q. (We used PROC UNIVARIATE in SAS, Statistical Analysis System).

Step 2. Estimate the relationship of l_o, σ, and q to m_i using multiple linear regression methods.

Step 3. Using the coefficients of the regression equations obtained in step 2 as initial parameter estimates, iteratively solve the system of m equations and n unknown coefficients to obtain a final set of parameters. The non-linear iterative phase of the model seeks a least-squares solution between the observed catches, n_{ij}, and the predicted catch of fish from the model (right hand side of the equation). We used PROC NLIN is SAS with the weighting factor, p_{ij}, and the following model:

$$n_{ij}=\frac{n_i}{\sigma\sqrt{(2\pi)}}\exp^{-(l_j-l_o)^2/2\sigma^2}x\left\{1-1/2q\sigma^{3/2}\left[\frac{(l_j-l_o)}{\sigma}-\frac{(l_j-l_o)^3}{3\sigma^3}\right]\right\} \qquad (1.2)$$

Step 4. Obtain an estimate of selectivity, s_{ij}, by inserting the final estimated set of n coefficients and the system of m functional

equations from step 3 into the assumed probability function.

Step 5. Standardize the ordinates, s_{ij}, of each curve by multiplying by the factor $d/max_i(s_{ij})$, where $max_i(s_{ij})$ is the ordinate at the mode of the curve and d is an arbitrary constant. This adjusts each curve to agree with the assumption that, at peak efficiency, nets of different mesh size are equally efficient.

Results and Discussion

The moments derived from the catch distributions of spotted seatrout varied systematically with increasing mesh sizes used in our experimental gang. The mean exhibited a strong positive linear relationship ($r^2 = 0.99$) while both the standard deviation and skewness varied across mesh as a second order polynomial (Figure 1.1). The coefficient of determination (r^2) was 0.98 and 0.96 for the standard deviation and skewness, respectively. The above functional relationships between the moments and mesh size provided the system of 3 equations and 8 initial parameter estimates used in the non-linear iterative phase of the model.

The final set of iteratively solved parameters from the non-linear phase of the model were, in general, close to the initial parameter values (Table 1.1). The precision associated with the final parameter solutions in Table 1.1 indicated good model performance. Additional indications of model performance are that generally no more than 100 iterations were needed to meet convergence and the final set of iteratively solved parameters in the model explained no less than 98%

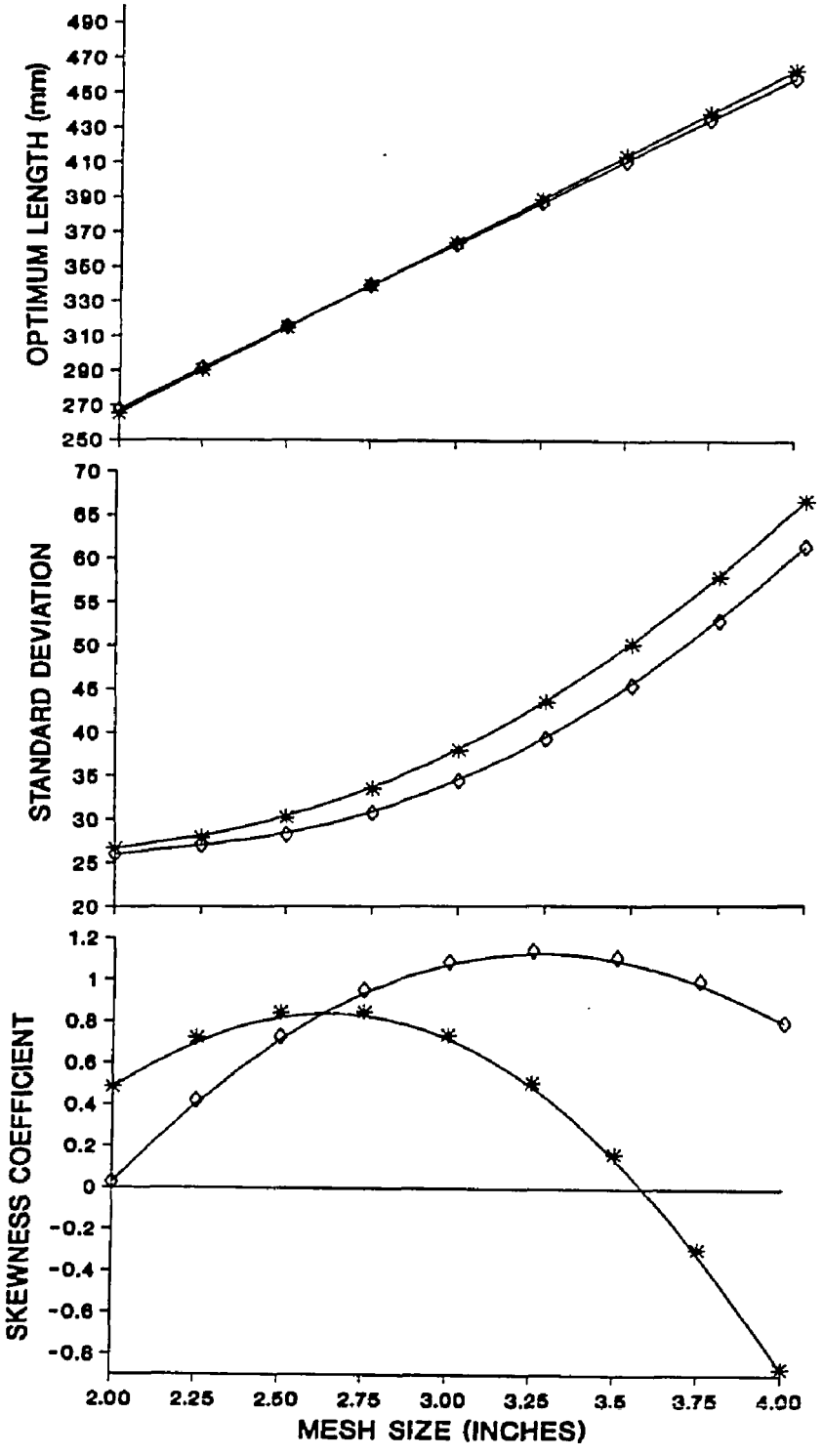

Figure 1.1. Comparison of the initial system of equations (stars) derived from the multiple linear regression to the final set of equations estimated from the non-linear iterative phase of the model.

of the total variation in the data. All 8 parameters used in the model were significantly different from zero with generally small asymptotic standard errors (Table 1.1). Five of the 8 initial values were within one standard error of the final parameters and all were within asymptotic 95% confidence intervals. The final set of equations represents an improvement over the initial parameter estimation as the weighted sums of squares were reduced by 74%. Relatively small differences between the initial and final equations, shown graphically in Figure 1.1, indicate stability in the final parameter solutions. No substantial differences are observed between these equations for the mean, although both initial coefficients (intercept and slope) were between the one and two standard error range of the final solution. The final solution to the equation for the standard deviation appears only slightly different from the initial coefficients, resulting in overall decreased values for all but the 2.0 inch meshes. The most pronounced differences appear to have occurred in the skewness coefficient equation. Here skewness coefficients corresponding to larger mesh sizes (3.0 through 4.0) shifted up while the two smaller meshes shifted down with all values being positive.

The above statistical considerations suggest that the system of 3 equations and 8 parameters used with the skew-normal model was suitable for the spotted seatrout data set used as an example here. This may be in part due to the robustness of the data set (large catches in the meshes fished). Poor precision associated with the parameter estimates and large changes between the initial and final functional equations may indicate instability due to small sample sizes in the meshes. In

Table 1.1. Model performance showing precision of the estimated coefficients for the final system of equations. Initial and final coefficients are compared to assess changes which result from the non-linear iterative phase of the model.

Parameter	Functional Form	Coefficient Initial	Coefficient Final	Asymptotic 95% Confidence Lower	Asymptotic 95% Confidence Upper
Mean	$\alpha + \beta_1 * m_i$	68.86	75.90	66.59	85.21
		99.20	95.81	91.78	99.83
Standard Deviation	$\alpha + \beta_1 * m_i + \beta_2 * m_i^2$	56.34	70.81	48.84	92.77
		-32.13	-41.42	-59.95	-22.88
		8.64	9.76	5.87	13.64
Skewness	$\alpha + \beta_1 * m_i + \beta_2 * m_i^2$	-5.61	-6.17	-9.17	-3.17
		4.91	4.45	2.13	6.78
		-0.93	-0.68	-1.12	-0.23

Model $r^2 = 0.98$

74% reduction in type III sums of squares

general, one should chose as simple a function as possible so as not to over-parameterize the model, particularly if the data set is not very robust.

From these final equations, the predicted catches derived from the model for each mesh were computed; the expected catches were in general agreement with the empirical data (Figure 1.2). The 2.0 and 2.5 inch meshes fit particularly well while slight departures are observed in the 3.0 and 3.5 inch meshes. Fits are poor with the 4.0 inch mesh, a condition which is probably in part due to the small numbers of fish caught in that mesh relative to the others and the observed bimodal catch distribution.

To the extent that the adjustments from the initial to final equations, using the weighting factor (p_{ij}) and this modeling approach, have filtered out the effects of unequal abundances the final set of equations inserted into the probability function should produce a fairly reliable representation of the selectivities. We feel that the effects of abundance are to some extent accounted for by the model and that the resultant curves (Figure 1.3), with the exception of the 4.0 inch mesh, should provide reasonable estimates of the mesh selection characteristics for spotted seatrout in coastal Louisiana. The selectivity curves shown in Figure 1.3 have been standardized (equal heights) under the assumption that the nets fish equally efficient. This assumption may not hold under biases due to net saturation or size-related avoidance by seatrout. We feel the run-around method employed in this study circumvents net saturation effects; particularly because catch rates were less than 25 fish per set for 90 % of the sets and

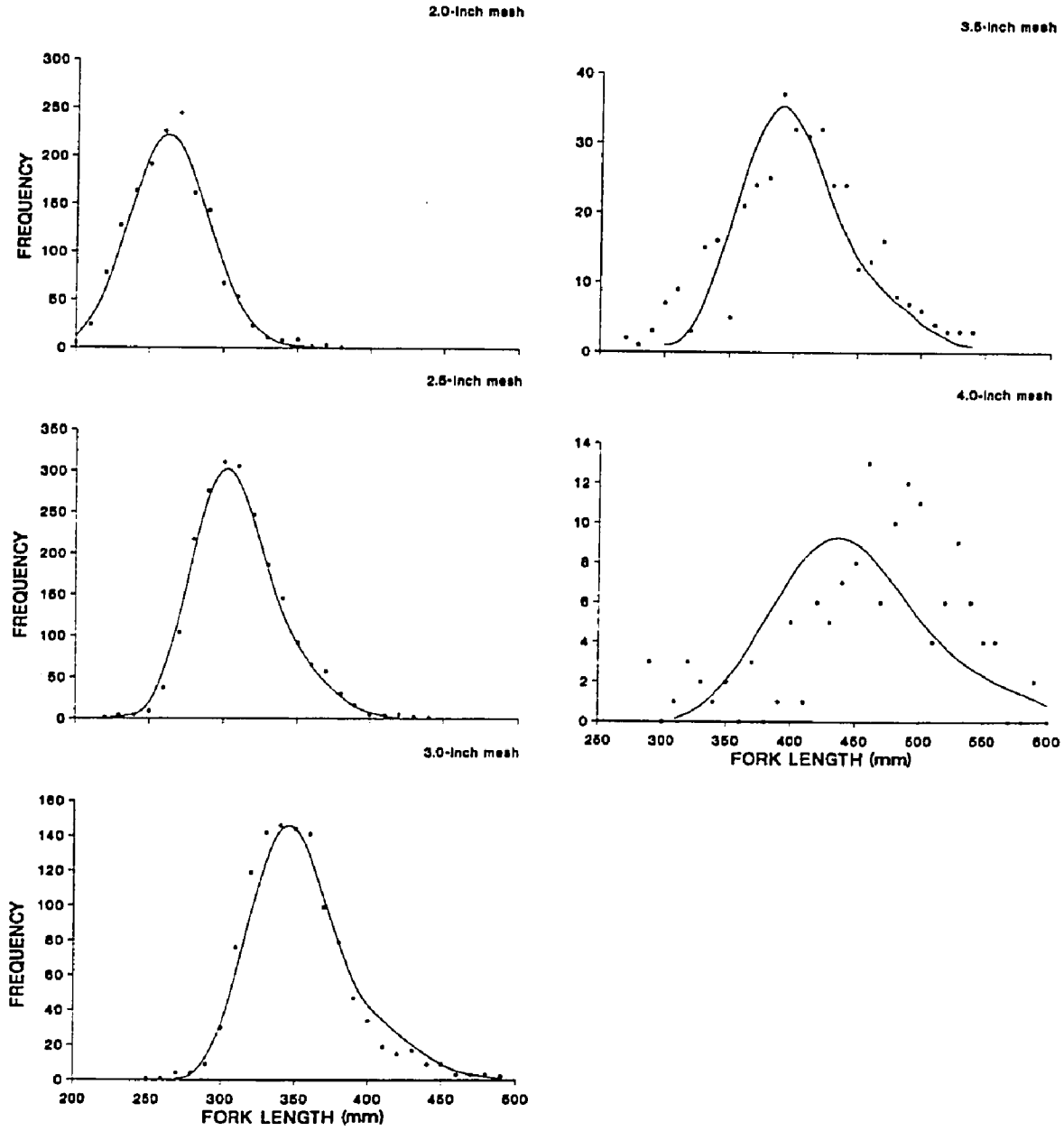

Figure 1.2. Comparison of predicted catches derived from the model (solid line) to the observed data (dots) for each mesh size in the experimental gillnet.

rarely exceeded 100 fish per set. Size-related avoidance by seatrout is much harder to assess with the data presented here, however we would like to address this question in the future. It should be noted from Figure 1.3 that these curves are not congruent, an assumption often implied in other indirect methods, and that the selection range increases with increasing mesh size. The relationship between optimum selection length (peak of the curve) and the size of mesh is clearly linear (Figures 1.1 and 1.3). This is a selection characteristic of interest in managing a gill net fishery, and its theoretical relationship was established by Baranov (1948), that $\phi = KL_m$, where ϕ is the mesh bar measure and L_m is the modal length of fish captured in it and K is called the selection factor. The regression line presented in Figure 1.1 is inverse to Baranov's relation. However, we computed the selection factor for spotted seatrout by regressing ϕ on L_m and found that $K = 0.13$ which was within the range of values found for slim bodied fishes (0.10) like mackerel to deep bodied fishes (0.20) such as bream (Andreev 1962). The theoretical line established here for spotted seatrout can be used to estimate similar optimum selection lengths for mesh sizes not included in this study.

The considerable overlap between selectivity curves from adjacent meshes (Figure 1.3) demonstrate that this particular configuration of gear is highly efficient at sampling the seatrout population as the probability of capture of fish within the mesh series is no less than 70 %. The mesh series used here should adequately sample the spotted seatrout population beginning from 250 mm (peak of 2.0 inch mesh) up to about 460 mm (peak of 4.0 inch mesh) which correspond to ages 3 and 6

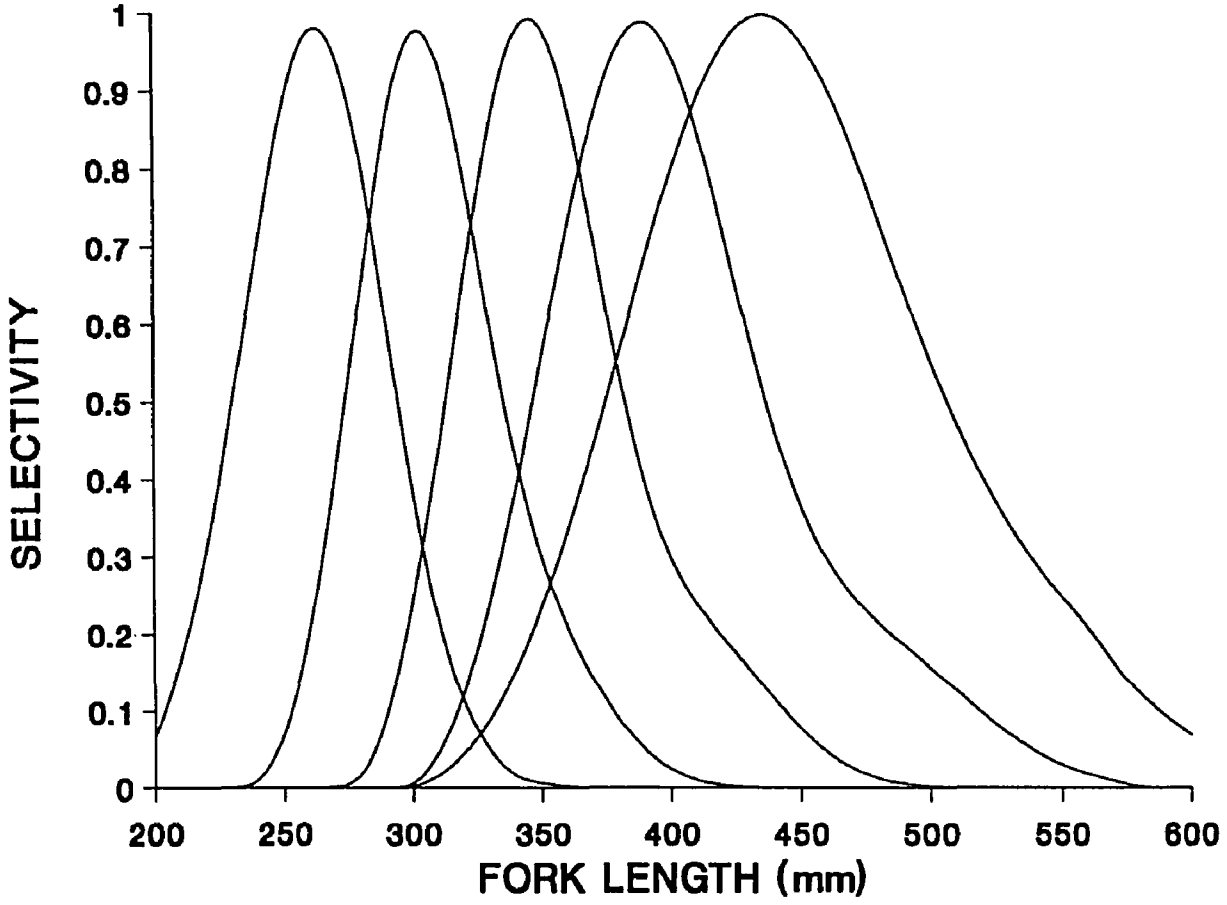

Figure 1.3. Estimated selectivity curves of the 2.0, 2.5, 3.0, 3.5, and 4.0 mesh size for spotted seatrout. The ordinate, selectivity, is standardized and represents the probability of capture.

for female and male fish, respectively (Weiting 1989). Thus, the effectiveness of this experimental gill net to sample older seatrout quickly diminishes beyond those ages; however, the relative population abundance for the various size classes of fish up to that size can be estimated. More reliable estimates of abundance will be derived from the selectivity curves within the size range where at least two meshes overlap sufficiently (250 to 500mm size range). Relative abundances were computed here following a convention similar to that of Gulland and Harding's (1961) graphical method and are computed as, $Nj = \Sigma(n_{ij}/S_{ij})$. The estimated relative population size-class abundance is plotted along with the experimental gill net catches in figure 1.4.

Caution should be used in interpreting the population size structure of spotted seatrout outside the specified range as small capture probabilities may lead to serious over-estimates of abundance. However, inferences concerning the population abundance within the 250 to 500 mm size range are possible and may provide useful information in the assessment of a fish stock. Here it is clear that the observed catches are similar to the true population abundance only over a short size range of fish (350-400 mm). Highest catches observed in the gill nets were in general not coincidental with highest abundances in the population and declines in abundance appear steeper than would be suggested from the catches.

The most striking feature of Figure 1.4 is the declining abundances of spotted seatrout from about 300 to 400 mm. These results may have two important management implications for this stock (as suggested from Figure 1.4). First, the dramatic declines in population

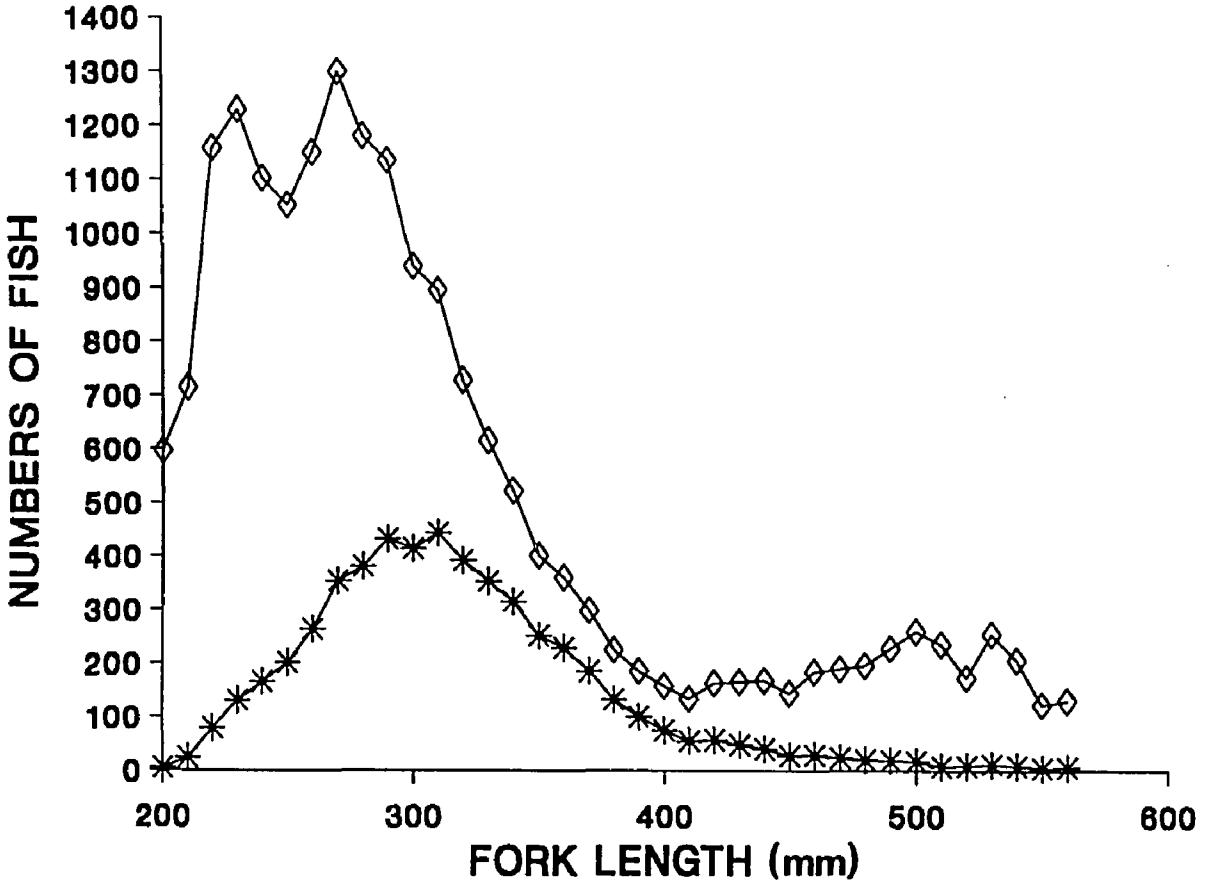

Figure 1.4. Observed 1988 experimental gillnet catches of spotted seatrout (stars) and the estimated relative abundances (diamonds) on the various size classes in the seatrout population.

abundance between 300 and 400 mm are coincident with the size at full recruitment to both the recreational and commercial fisheries for spotted seatrout in Louisiana. Secondly, the most significant spawning contribution to stock replenishment is from females whose length is greater than 400 mm (Arnoldi 1984; Weiting 1989). If the removal of fish from the spotted seatrout population is indeed due to the combined exploitation by the recreational and commercial fisheries, then resource managers may wish to consider management measures to ameliorate fishing mortality within this size range where female seatrout have not yet reached their full spawning potential.

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CHAPTER II

A Method of Estimating the Size Composition of a Fish Population And a Development of Variance Estimators, with an Example for Spotted Seatrout, *Cynoscion nebulosus*.

Introduction

The estimation of the size composition of a fish population is important to the study of a stock's dynamics and the management of a species. Numerous types of fishing gears have been employed to sample the size composition of a fish population, however most gears are highly size selective and bias in population descriptors such as growth, mortality, and abundance can be introduced. Experimental gillnets are commonly used sampling devices which, to some extent, circumvent size selective biases by fishing a series of different sized meshes simultaneously so that a broader range of sizes of fish in the population are captured. Even this, however, does not ensure a truly representative sample of the fish population and effort must be made to correctly estimate the selectivity of each mesh in the experimental gillnet before an estimate of abundance can be obtained.

Once selectivity is estimated, the catches of fish in the experimental gillnet can be adjusted for the effect of mesh selectivity, thereby giving an estimate of the relative abundance or length composition of the population from which the sample was drawn (Olsen 1959; McCombie and Fry 1960; Gulland and Harding 1961). Most applications of estimating gillnet selectivity used today still rely on the earlier methods due to a lack of newer approaches, and those studies

which have used the selectivities of the meshes to estimate the size composition of the population do not provide variances associated with those estimates.

Since Baronov's (1948) pioneering work on gillnet selection theory, a myriad of methods and models have been proposed to estimate the selectivity of gillnets; with Regier and Robson (1966) and Hamley (1975) providing a review of these earlier approaches. Since this earlier work, few fundamentally different approaches have been proposed (Boy and Crevelli 1988; Helser et. al 1991).

In an earlier work (Helser et al. 1991), we viewed gillnet selectivity as a process of capture which varies systematically as a function of size-class of fish and mesh size. To mathematically describe this capture process, we used an iterative nonlinear maximum likelihood fitting procedure to fit the gillnet catches of fish size-class j in mesh i. The model solution is a set of parameter estimates describing the response surface as the probability of capture for fish of size-class j in mesh size i. Among a number of advantages cited from this new approach, and perhaps the most notable, is that the assumption of a particular mathematical model used to describe selectivity and the precision of the resulting parameter estimates can be assessed, as the nonlinear least-squares algorithm provides variance estimates. We now extend the utility of this modeling approach one step further by using the output from the nonlinear maximum likelihood algorithm to estimate variances associated with the estimated relative abundances.

In this paper, we first modify a recently described method of estimating gillnet selectivity and population size structure which uses a non-linear iterative least squares approach (Helser et al. 1991). Since the original development of this method, two additional years of data have become available with which we examine the consistency of the modeling approach and the variation in the model parameter estimates over time. We use the model parameter estimates derived from the non-linear minimization algorithm to estimate the relative abundances of the various size-classes of fish in the population and present a variance estimation procedure to derive confidence intervals about those estimates. These methods are again applied to the experimental gillnet catches of spotted seatrout (*Cynoscion nebulosus*) from 1988 to 1990, and we examine the population size structures for the different years and sexes by year as well as interannual variation of those estimates in coastal Louisiana.

Materials and Methods

Review of the Model

The indirect estimation of gillnet selectivity uses the catches of fish captured in a series of different meshes, fished simultaneously, so that some unknown proportion of the various size-classes of fish available in the population are retained in the gear. Selectivity is the quantitative expression to the unknown proportion and is usually represented as the probability of capture of a certain size fish in a given size of mesh. Helser et al. (1991), using the skew-normal

probability density function to mathematically describe selectivity, have developed a non-linear iterative approach which seeks a least squares solution between the expected catch based on the model and the observed catch of fish. Their model is given mathematically as:

$$n_{ij}=\frac{n_i}{\sigma\sqrt{(2\pi)}}\exp^{-(l_j-l_0)^2/2\sigma^2}x\left\{1-1/2q\sigma^{3/2}\left[\frac{(l_j-l_0)}{\sigma}-\frac{(l_j-l_0)^3}{3\sigma^3}\right]\right\} \qquad (2.1)$$

where:

l_o = mean size of fish caught in mesh size i.

σ_i = standard deviation of the catches of fish size - class j in mesh i.

q_i = skewness coefficient of the catches of fish size - class j in mesh i.

l_j = mean size of fish in size-class j.

m_i = size of mesh i, specifically stretch measure in inches.

n_{ij} = catches of fish of size-class j in mesh i.

$n_i = \sum_i n_{ij}$.

Any number of other probability distributions can be used in place of (2.1), however, we chose this particular function because of the pronounced skew associated with the distributions of seatrout catches from the meshes in our experimental gang. Moreover, this model has the advantage of expressing its parameters: the mean, standard deviation, and skewness separately in terms of increasing mesh size which allows maximum flexibility in examining the functional relationship of each term. For instance, in our case for spotted seatrout we found a system of m initial equations to express the functional relationship of l_o, σ,

and q across m_i; where l_o is a linear and σ, and q are quadratic functions of m_i. The resulting equation (2.1) is an eight parameter model which simultaneously fits n_{ij} for fish of size-class j in mesh size i using a maximum likelihood estimation procedure. At this point, the final parameter estimates from the nonlinear iterative phase of the model can be examined for the potential for reducing the model to a more simple symmetric normal distribution to describe selectivity. After this process, selectivity is obtained by inserting the estimated set of parameters from the non-linear iterative phase of the model into the assumed probability function.

We subsequently made a modification to (2.1) by dividing both sides of the equation by n_i. The resulting left hand side of (2.1) now becomes $p_{ij} = n_{ij}/n_i$, where p_{ij} is the percent relative frequency of fish size-class j caught in mesh size i. Since we were ultimately trying to estimate selectivity, expressed as a probability, fitting p_{ij} instead of the observed catch (n_{ij}), provides a more direct estimate. We noted that after fitting the equation for p_{ij} the residuals were more homogeneous than with the fits obtained from the original equation 2.1. The error variance was apparently correlated to size-class of fish, though this may be more a function of abundance (numbers caught in a given size-class) than of length of fish as numbers available to capture decrease with increasing length. Since n_i (equation 2.1) is the number of fish caught with a given mesh size, whose optimum selection length increases and magnitude decreases with larger meshes, dividing both sides of equation 2.1 by n_i seems to normalize this problem.

After fitting, each curve was then standardize by the factor $d/\max_i(s_{ij})$, where $\max_i(s_{ij})$ is the ordinate at the mode of the curve and d is an arbitrary constant (i.e. 1.0). This adjusts each curve such that, at peak efficiency, nets of different mesh size are equally efficient. Finally, using the standardized selectivities (S_{ij}), relative abundances were computed as $N_j = \Sigma[n_{ij}/S_{ij}]$, where $S_{ij} = s_{ij}/\max_i(s_{ij})$ and can be rewritten as

$$N_j = \frac{n_{ij}}{s_{ij}/max_i(s_{ij})} = \sum_1^n \frac{[(n_{ij} * max_i(s_{ij}))]}{s_{ij}} \qquad (2.2)$$

A second modification to the procedure was made which involved the expansion of the catch to relative abundances given in (2.2). Small capture probabilities, $s_{ij}/\max_i(s_{ij})$, in (2.2) can lead to unrealistically high relative abundance estimates, especially those probabilities which result from fitting the tails of the catch distributions for the various meshes. Therefore, in an effort to standardize the estimation of relative abundances the estimated capture probabilities for a given size-class of fish in a given mesh which were less than 0.10 were excluded from the computation (i.e. $s_{ij}/\max_i(s_{ij})<0.10$). In general, this procedure retained up to the 90^{th} percentile of each mesh's catch distribution while omitting estimates from the tails where fits to the observed data were poorer. The forementioned modifications to the procedure are likely to produce differing results, both in the estimation of model parameter estimates

and relative abundances, than those obtained earlier in Helser et al. (1991). These differences will be discussed in their appropriate sections.

Variance Estimation

The relative abundance in (2.2) is computed as the summation of the numbers of fish of size-class j which must have encountered the net of mesh i to observe the catch, n_{ij}. For the purposes of estimating variances described here, we assume the numerator in (2.2) is a constant. The variance then is associated with the random variable, s_{ij}, in the denominator of (2.2) which will take the form of the variance of a quotient. An approximate formula for the variance of a quotient, var[X/Y], is obtained from a Taylor series expansion where only the second order terms are retained and is given (Mood et al. 1974) as

$$var\left[\frac{X}{Y}\right] \approx \left(\frac{\mu_x}{\mu_y}\right)^2 \left(\frac{var[X]}{\mu_x^2} + \frac{var[Y]}{\mu_y^2} - \frac{2cov[X,Y]}{\mu_x \mu_y}\right) \qquad (2.3)$$

The second and fourth terms in (2.3) drop out since the var[X] = 0 and we assume cov[X,Y] = 0, leaving

$$var\left[\frac{X}{Y}\right] \approx \left(\frac{\mu_x}{\mu_y}\right)^2 \left(\frac{var[Y]}{\mu_y^2}\right) \qquad (2.4)$$

And substituting the variables and constants from (2.2) into (2.4) we obtain

$$var\left[\frac{n_{ij}*max_i(s_{ij})}{s_{ij}}\right]\approx\left(\frac{n_{ij}*max_i(s_{ij})}{s_{ij}}\right)^2\left(\frac{var[s_{ij}]}{s_{ij}^2}\right) \qquad (2.5)$$

Then rewriting (2.5) and summing over mesh i provides the variance of the estimated relative abundance, N_j, of fish in size-class j from the fished population

$$var[N_j]=var\left[\frac{n_{ij}*max_i(s_{ij})}{s_{ij}}\right]\approx\sum_{i=1}^{n}\left(\frac{[n_{ij}*max_i(s_{ij})]^2}{s_{ij}^4}\right)(var[s_{ij}]) \qquad (2.6)$$

To derive a variance of the sum (N_j), we must first obtain the sum of the variances of the random variable, s_{ij}, which are non-linear functions of the model parameters, θ. The maximum likelihood estimate of θ, labeled $\hat{\theta}$, is the set of parameters which minimizes the sum of the squared residuals for normally distributed errors

$$SS[Res(\hat{\theta})] = \Sigma[Y_i - f(x'_i,\hat{\theta})]^2 \qquad (2.7)$$

where, $f(x'_i,\hat{\theta})$ is the functional form of (2.1) evaluated at the n values of x_i'. Explicit solutions for $\hat{\theta}$ cannot, in general, be obtained because the partial derivatives of a nonlinear model are functions of the parameters and the resulting "normal equations" are themselves nonlinear (Rawlings 1988). The partial derivatives of SS[Res($\hat{\theta}$)], with

respect to each parameter of $\hat{\theta}$ are set equal to zero to obtain the "normal equations" which are of the general form

$$\frac{\partial SS[Res(\hat{\theta})]}{\partial \theta_j} = -\Sigma [Y_j - f(x_j', \hat{\theta})] \left[\frac{\partial f(x_j', \hat{\theta})}{\partial \theta_j} \right] = 0 \qquad (2.8)$$

where the second set of brackets contain the partial derivatives of the functional form of model (2.1). Due to the complexity of (2.1), we obtained partial derivatives using a numerical procedure called "REDUCE" (Hearn 1983) in Fortran on a 3038 IBM mainframe computer. These equations are cumbersome, so here, and in Helser et al. (1991), we used the derivative-free Multivariate secant method (Ralston and Jennrich, 1978) to arrive at maximum likelihood solutions to $\hat{\theta}$. This approach uses an iteration history where equation (2.7) is evaluated at each iteration as the values of $\hat{\theta}$ are changed.

The nonlinear model (2.1), modified to fit p_{ij}, was used for all analyses. We ran the nonlinear gillnet selectivity estimation procedure as described in Helser et al. (1991) and obtained model parameter estimates for, $\hat{\theta}$, for the different years and for the sexes separate by year. Evidence was available to suggest that male and female spotted seatrout have different parameter estimates. Years and sexes by year were tested for differences in $\hat{\theta}$ using the Likelihood ratio test (Gallant 1987).

Once estimated, the variance-covariance matrix of $\hat{\theta}$ can be recovered from the nonlinear maximum likelihood program output from, $s^2(\hat{\theta}) = SpS$, where S is the pxp diagonal matrix of asymptotic standard errors, p is the estimated asymptotic correlation matrix, and

$s^2(\theta) = SS[Res(\theta)]/(n-p)$ (Rawlings 1987). $SS[Res(\hat{\theta})]$ has approximately a chi-square distribution with n-p degrees of freedom and asymptotic arguments can be used to show asymptotic normality of $\hat{\theta}$ as n gets large. Sample sizes used in this analysis were probably more than adequate (n > 100 in almost all cases) to ensure asymptotic normality of the parameter estimates. Problems can, however, arise when final parameter solutions obtained from one round of iterations are used as starting values for another run of iterations. This is common practice for obtaining a desired level of parameter estimate precision. Here, a second or even a third run may result in an incomplete correlation matrix. This is probably the result of an inadequate iteration history, since the "second run" typically requires fewer iterations to reach convergence of a "global solution" and since the Multivariate Secant Method computes numerical estimates of the derivatives from the iteration history. An alternate approach to estimating the variance-covariance matrix of $\hat{\theta}$, and one in which we always obtained stable results, is using

$$s^2(\hat{\theta}) = (F'F)^{-1}s^2 \qquad (2.9)$$

where F is the nxp matrix of partial derivatives evaluated at n data points x_i'(Gallant 1987). We preferred using (2.9) to estimate the variance-covariance of $\hat{\theta}$ based on the above considerations, although both approaches yielded similar results, particularly for model parameter estimates with smaller asymptotic standard errors.

Once estimated, we used the variance-covariance matrix, F'F, to estimate another nonlinear function of θ. Here, we wanted to estimate

the variance of the fitted values or the probabilities, $s_{ij} = f(\hat{\boldsymbol{\theta}})$, which are nonlinear functions of $\boldsymbol{\theta}$. For each size-class and mesh size, let $h(\boldsymbol{\theta})$ be any nonlinear function of $\boldsymbol{\theta}$. Gallant (1987) has shown that $h(\hat{\boldsymbol{\theta}})$ is approximately normally distributed with mean $h(\boldsymbol{\theta})$ and variance $\mathbf{H}(\mathbf{F}'\mathbf{F})^{-1}\mathbf{H}'\sigma^2$, where

$$\boldsymbol{H}=\left(\frac{\partial[h(\boldsymbol{\theta})]}{\partial\theta_1}\ \frac{\partial[h(\boldsymbol{\theta})]}{\partial\theta_2}\cdots\frac{\partial[h(\boldsymbol{\theta})]}{\partial\theta_p}\right) \tag{2.10}$$

is the row vector of partial derivatives of the function $h(\boldsymbol{\theta})$ with respect to each of the parameters and $\mathbf{F}'\mathbf{F}$ is the variance-covariance matrix of $\hat{\boldsymbol{\theta}}$ of full rank. Thus, we can estimate the variance of $h(\hat{\boldsymbol{\theta}})$ by

$$s^2[h(\hat{\boldsymbol{\theta}})] = [\mathbf{H}(\mathbf{F}'\mathbf{F})^{-1}\mathbf{H}']s^2 \tag{2.11}$$

using the first-order terms of a Taylor series expansion to approximate $h(\hat{\boldsymbol{\theta}})$ with a linear function. This calculation can be programmed and estimated directly. However, tedious large matrix multiplication of (2.11) can be circumvented, and the same result obtained, by recovering the diagonal hat matrix from PROC REG (SAS 1985) for the regression of H as the independent variable on any dummy dependent variable (i.e. 1). The leverage, $x_i(X'X)^{-1}x'_i$, from the regression output is equivalent to $\mathbf{H}(\mathbf{F}'\mathbf{F})^{-1}\mathbf{H}'$ in (2.11) and multiplication by the nonlinear regression estimate of the mean square error will give $s^2[h(\hat{\boldsymbol{\theta}})]$.

A 100(1-α)% confidence interval of $h(\theta)$ is approximated as

$$h(\hat{\theta}) = t_{[\alpha,(n-p)]}[H(F'F)^{-1}H's^2]^{1/2} \qquad (2.12)$$

We compute 95% confidence intervals to express the variation around the estimated relative abundances of the various size-classes of fish in the population.

Results and Discussion

Model Modification

The modification to equation 2.1 (fitting n_{ij}/n_i) we present here to estimate the selectivity of gillnet meshes represents an improvement over the original approach (fitting n_{ij}) in that the model error was substantially improved for non-homogeneous error variance. Figure 2.1 shows the effect of the modification on improving the constancy of the error variance with respect to size-class of fish (l_j) for the 1988 gillnet data. Homogeneous error variance for a nonlinear (or linear) regression model is a required assumption for parametric hypothesis testing and the computation of confidence intervals. Moreover, the normalization of the residuals by the modification of the dependent variable (n_{ij}/n_i) probably augments the normality assumption for the model parameters using this nonlinear maximum likelihood estimation routine. The cost of this improvement in the model's error variance was a slight reduction in the model r^2 value, going from 0.99 before to 0.97 after the modification.

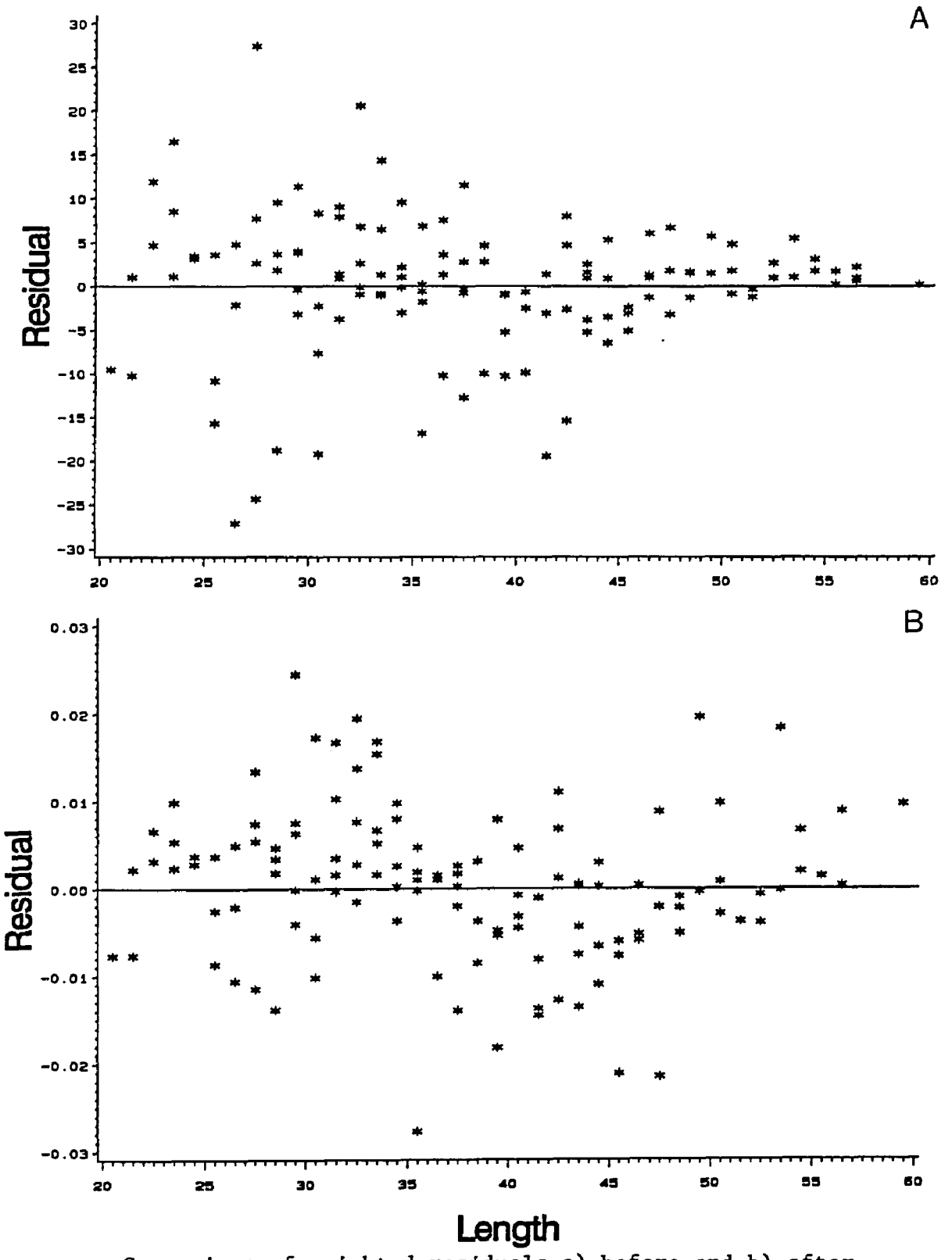

Figure 2.1. Comparison of weighted residuals a) before and b) after model modification.

Although not shown here, parameter estimates obtained from fitting the original equation (2.1) are very similar to those of table 1 of Helser et al. (1991). Comparison of the model parameter estimates for the 1988 data in table 2.1 (this paper) with those originally obtained in Helser et al. (1991) indicates that slight changes were observed in some of the model's parameter estimates after the modification, particularly those related to the optimum selection length (mean) and the skewness coefficient. These changes appear to accompany an overall better fit to the observed data, especially for the larger mesh sizes. It should be noted that the parameters for the mean (optimum selection length) and the standard deviation given earlier (Helser et al. 1991) appear one decimal place larger than those of table 2.1 because size-class categories used in the original analysis were in millimeters, and we subsequently used centimeters. The only affect size-category scaling has on the analysis is the position of the decimal for the mean and standard deviation, since these are directly related size-class, whereas the skewness term is not.

Model Selection Parameters

Gillnet selectivity, as expressed by our model selection parameters, is probably not constant through time, but varies with changes in those factors which determine the selection process on individual fish. The morphometry of a fish is probably the most important factor governing the selection process and one upon which selection theory is based (Baronov 1945). Therefore, environment and the internal dynamics of the fish population may affect this process.

It is also possible, however, that the size/age structure of the fish population also plays a role on the selection process, and changes in the selection parameters may reflect a change in the population size structure as well as changes in fish morphometry.

In this study, we felt it was important to explore variation in the model parameter estimates through time, therefore data was analyzed by year from 1988 to 1990. Since relative abundances are estimated from the model parameter estimates, individual year's parameter estimates were used in that computation to more accurately reflect the population size-class abundance in a given year. The time-averaged model (pooling data across the three years) in the analysis reflects steady state conditions in selection parameter estimates and is used to compare population size structures derived from year-specific and time-average models. This comparison should facilitate analysis of the relative accuracy in the estimation of relative abundances of the various size-classes of fish in the population.

The nonlinear iterative modeling approach, modified to fit p_{ij} worked quite well for the available data from 1988 to 1990, and for all years combined. All model parameter estimates for the different years and for years combined were significantly different from zero ($p < 0.025$). Coefficients of determination (r^2) where generally high for 1988, 1989, and for the overall model (>0.97), but considerably less for 1990 (>0.87). Table 2.1 gives model parameter estimates for each year, and for the years combined along with asymptotic standard errors and model coefficients of determination (r^2). The parameter estimates relating to the optimum selection length (μ_0 and μ_1) were generally more

Table 2.1. Comparison of model selection parameter coefficients, along with asymptotic errors and model r^2 for gillnet data from 1988 through 1990. Parameter estimates from time-averaged model (years combined) also included.

	1988	1989	1990	years combined
Parameter	Coefficient (asymptotic standard error)			
μ_0	6.665(0.296)	6.789(0.445)	4.163(0.732)	6.747(0.392)
μ_1	10.002(0.114)	10.077(0.166)	11.149(0.285)	10.079(0.147)
S_0	5.843(0.875)	14.868(0.603)	6.831(1.884)	10.031(0.663)
S_1	-3.138(0.651)	-9.599(0.440)	-3.779(1.397)	-6.020(0.715)
S_2	0.791(0.115)	1.926(0.135)	0.886(0.250)	1.278(0.084)
q_0	-13.220(0.936)	-5.269(0.992)	-4.098(2.040)	-4.771(0.440)
q_1	10.017(0.643)	4.767(0.679)	4.252(1.384)	4.362(0.275)
q_2	-1.722(0.105)	-0.883(0.109)	-0.858(0.226)	0.804(0.046)
Model r^2	0.97	0.97	0.87	0.97

consistent between the three years than those relating to the selection range (standard deviation; s_0, s_1, and s_2) and the skewness (q_0, q_1, and q_2). The likelihood ratio test (Mendenhall et al. 1986) indicated that the model parameter estimates were significantly different between the years ($p<0.01$). The selection parameters for those models which contribute more to interannual differences are examined in figure 2.2, and show the functional relationship between the optimum selection length, standard deviation and skewness coefficient with respect to increasing mesh size by year. The optimum selection length varies little between years, except perhaps for the larger mesh sizes, where the largest difference between any given year is at most 2.0 cm. The standard deviation (selection range) differs more between years than the optimum selection length where the selection range appears to increase more with increasingly larger mesh sizes for 1989 than the other two years. Most prominent, though, are the differences in the functional relationships of the skewness coefficient terms between the years (figure 2.2). The skewness coefficient appears to be more dissimilar for any two years than for the other model selection parameters, which probably accounts principally for the significant annual differences in the parameter estimates of the year-specific models.

The annual differences in the selectivity curves for the various meshes themselves are not, however, too dissimilar as indicated from figure 2.3. Figure 2.3 shows the predicted probability of capture for the first four meshes in the experimental gang compared by year. Slight shifts in the curves, to larger or smaller size fish, seem to occur from one year to the next without great deviations in the actual curve

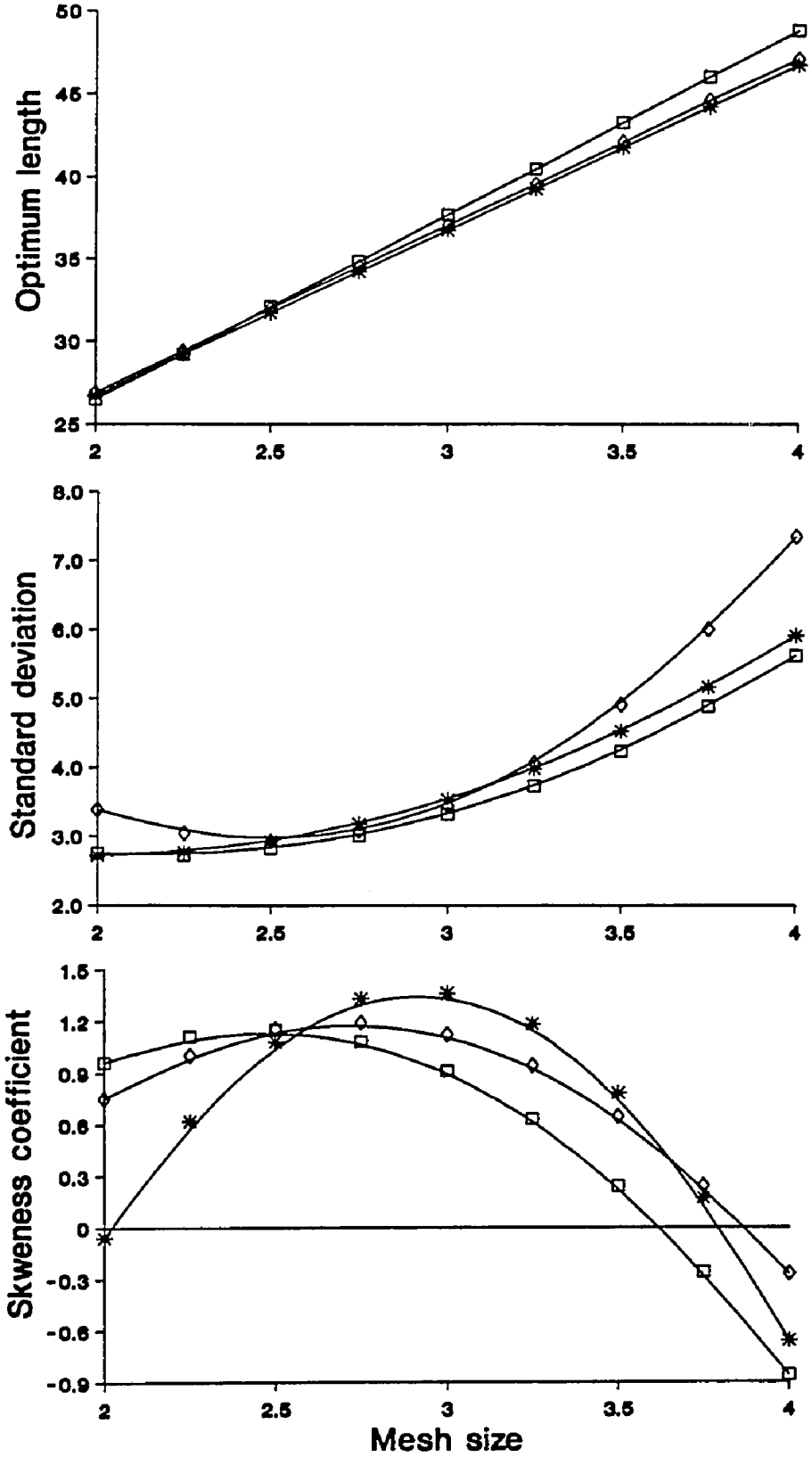

Figure 2.2. Shows the functional change in the model selection parameters with respect to increasing mesh size between 1988 (star), 1989 (diamond), and 1990 (square).

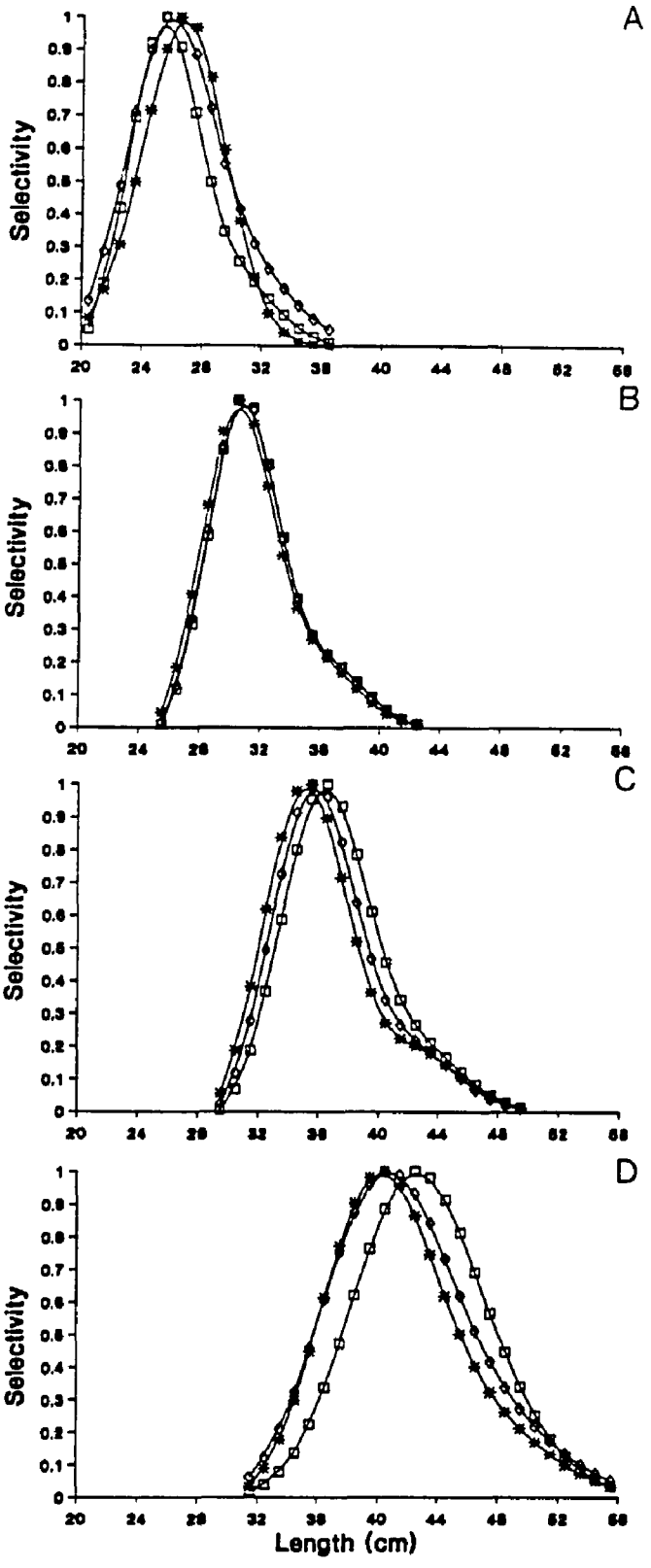

Figure 2.3. Shows annual differences in the estimated selectivity curves for the a) 2.0, b) 2.5, c) 3.0, and d) 3.5 inch mesh sizes between 1988 (star), 1989 (diamond), and 1990 (square).

shapes. These shifts may be the result of recruitment changes or changing population size structures from one year to the next or perhaps changes in fish morphometry related maturation and/or condition. Changes in individual fish condition would effect the selection properties more directly.

In any case, a model was fit to the years combined in an attempt to average over spurious annual differences related to changing recruitment and population size structures. The fit of the overall model to the observed data was very good, giving actually better model parameter precision for most parameters than obtained from the years separately. Figure 2.4 shows a comparison of the observed relative frequencies of the catches by year for the various meshes along with the predicted relative frequency for the overall model. Interannual variation in the relative frequencies appear to be more extreme in the largest two mesh sizes in figure 2.4, especially in the 1990 gillnet catches. This variation in 1990 is probably due to a much lower overall catch for larger size-classes of seatrout than for the two earlier years. Further, a conspicuous shift in the peak relative frequency to smaller size-classes of fish for the 2.0 inch mesh is seen in 1990 in figure 2.4.

If the same graph is constructed for males and females separately (figures 2.5 and 2.6, respectively), it appears that the shift in peak relative frequency seen in figure 2.4 is due primarily to male spotted seatrout. Here the prominent peak in male abundance at the 24.5 cm size-class shown in figure 2.5 translates into a shift in the optimum selection length for the 2.0 inch mesh in 1990 to a smaller size of fish

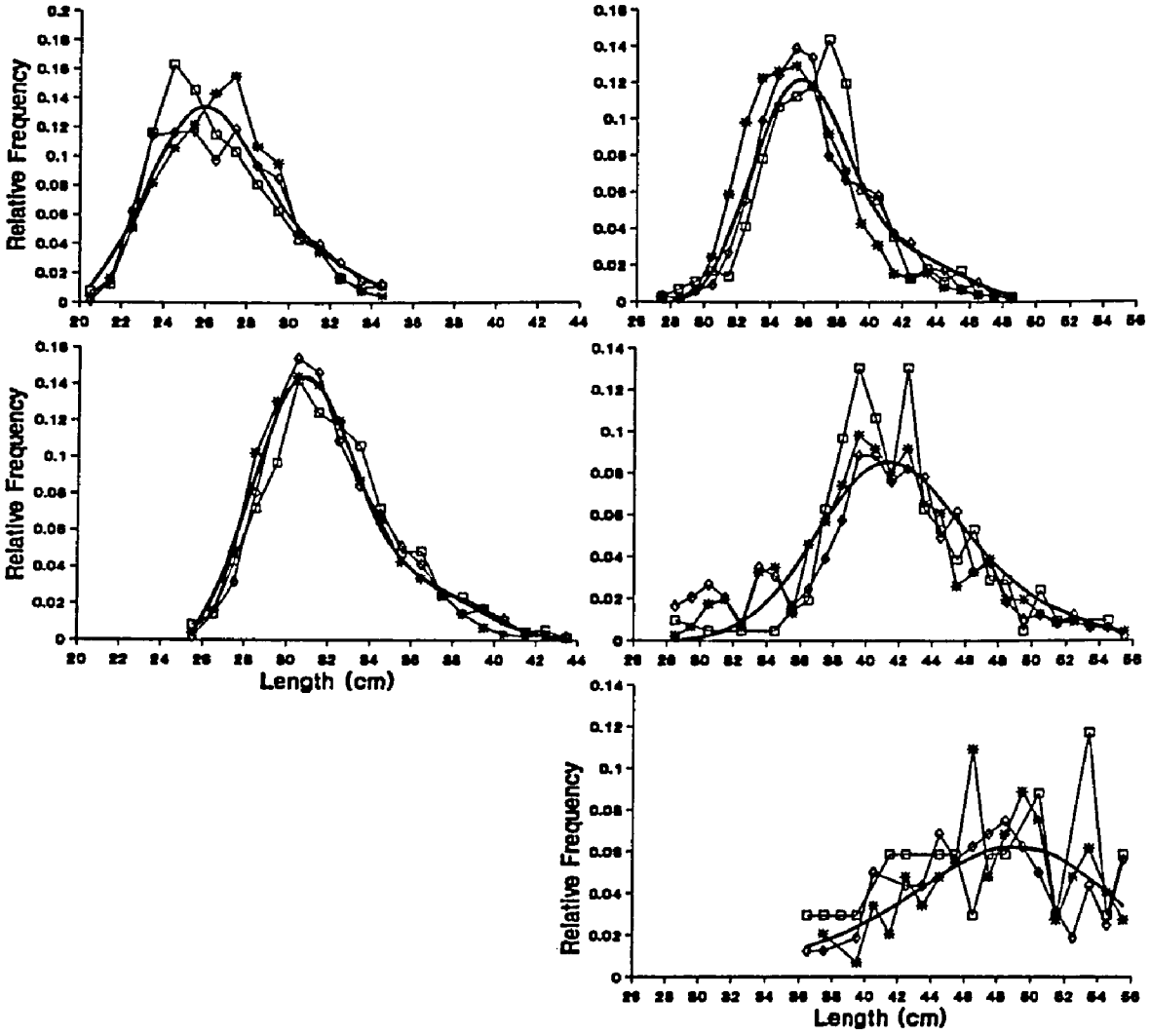

Figure 2.4. Comparison of observed and predicted relative frequencies (percent) for sexes combined caught in the various meshes of the experimental gillnet. Predicted values, estimated from time-average model, are given as solid dark lines and compared to individual year values for 1988 (star), 1989 (diamond), and 1990 (square).

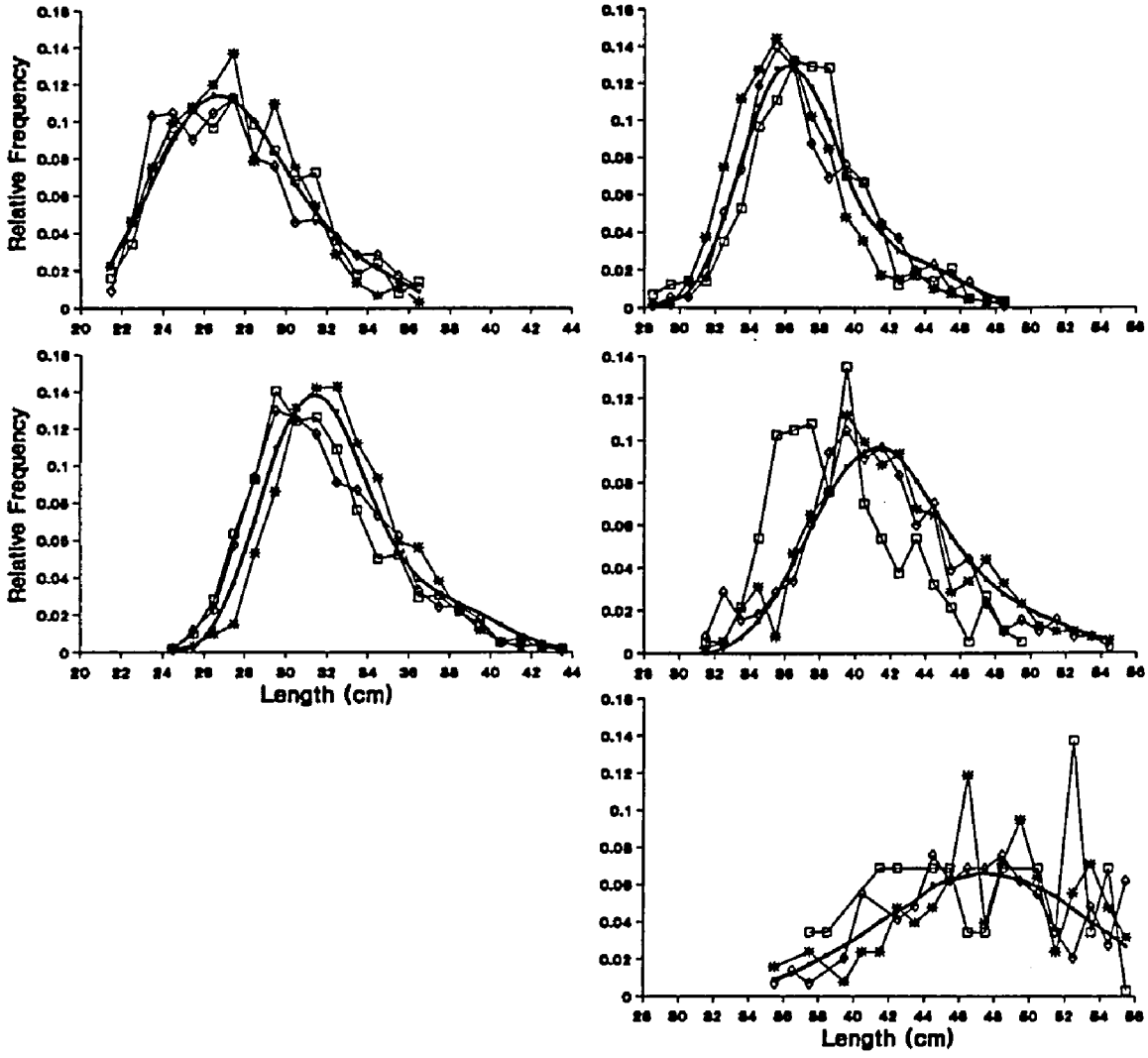

Figure 2.5. Comparison of observed and predicted relative frequencies (percent) for female seatrout caught in the various meshes of the experimental gillnet. Predicted values, estimated from time-average model, are given as solid dark lines and compared to individual year values for 1988 (star), 1989 (diamond), and 1990 (square).

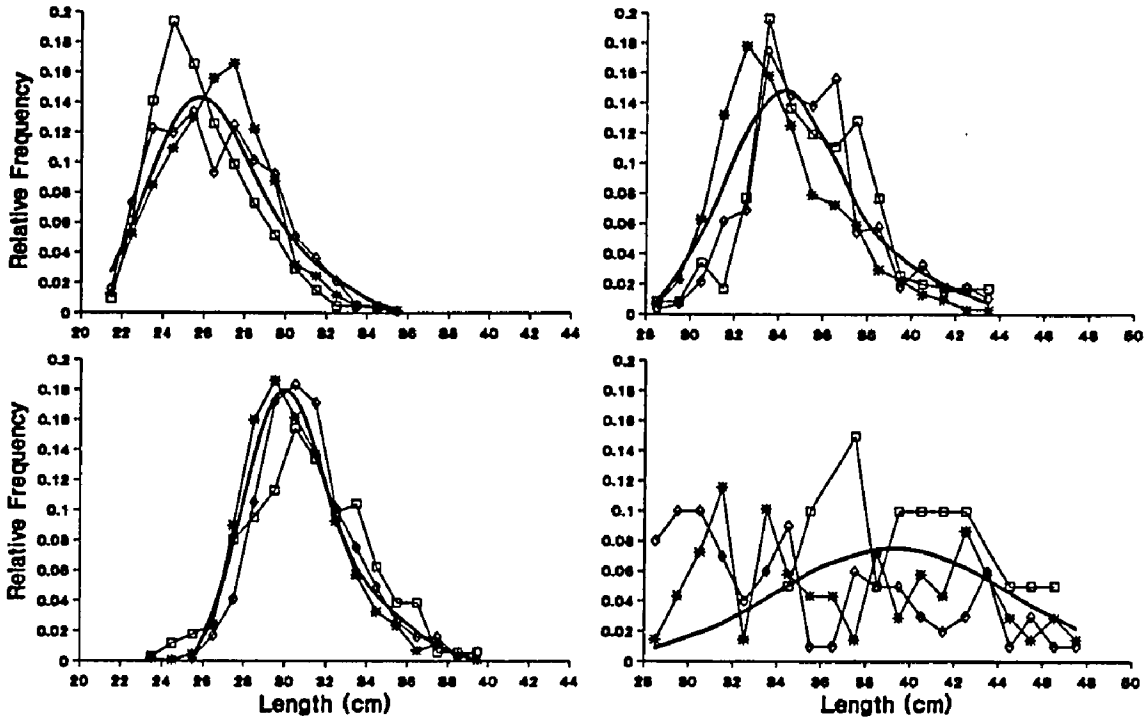

Figure 2.6. Comparison of observed and predicted relative frequencies (percent) for male seatrout caught in the various meshes of the experimental gillnet. Predicted values, estimated from time-average model, are given as solid dark lines and compared to individual year values for 1988 (star), 1989 (diamond), and 1990 (square).

over the two earlier years. A possible explanation for the observed shift in peak catch in the 2.0 inch mesh from 1988 to 1990 is a pulse in recruitment of smaller male fish into the gear, possibly attributable to a minimum size regulation (increase to 30.0 cm) imposed on the fishery in 1987. Another explanation, and one which we were able to examine with the available data, is that there may have been an increase in the condition of spotted seatrout between 1988 and 1990. Length-weight relationships for male and female spotted seatrout by year were fit to the experimental gillnet data to compare changes in condition factors. Table 2.2 shows length-weight regression coefficients for male and female spotted seatrout from 1988 to 1990. Analysis of covariance indicated a significant difference in the slopes between years and sexes ($p < 0.05$). Because of differing slopes, condition factors between years are not directly comparable (LeCren 1951). However, the data presented in table 2.2 suggests that for a given size of male spotted seatrout (i.e. 24.5 cm size-class were the peak abundance occurs in 1990) the predicted weight increases from 139 grams in 1988 to 162 grams in 1990. Data was available to convert weight to maximum fish girth from a morphometric study of seatrout conducted between 1981 and 1982. Based on a regression of girth to weight (table 2.2) a male spotted seatrout weighing 139 grams and a 162 grams is approximately 11.1 cm (1988) and 11.6 cm (1990) at its maximum girth, respectively. The difference in maximum girths between 1988 and 1990 translates into a girth-perimeter ratio of 1.09 and 1.14, respectively, for the 2.0 inch mesh. This difference in girth-perimeter ratio implies that the optimum selection length for male seatrout in

Table 2.2. Morphometric relationships for male and female spotted seatrout data obtained from gillnets between 1988 and 1990. Shown are weight-length regressions by year along with sex-specific girth-weight regressions. Computations illustrate the change in approximate weight, girth, and girth-perimeter ratio (G/P ratio) of a 24.5 cm male spotted seatrout.

	Weight-length Regressions			Girth-weight Regressions Males: $28.13*(\text{weight})^{0.278}$, ($r^2$=0.96) Females: $24.24*(\text{weight})^{0.302}$, ($r^2$=0.94)		
Year	Intercept	slope	r^2	Approx. weight (gm)	Approx. girth (cm)	G/P ratio
		Males				
1988	-4.35	2.92	0.88	139	11.1	1.09
1989	-4.45	2.95	0.91	146	11.2	1.10
1990	-4.82	3.10	0.92	162	11.6	1.14
			Females			
1988	-4.46	2.96	0.94			
1989	-4.83	3.05	0.96			
1990	-4.61	2.99	0.93			

1990 should on the average be at a smaller size than that observed in 1988. Figure 2.6 confirms this observation as peak relative frequency for male in the 2.0 inch mesh in 1990 is shifted to smaller size class than the earlier two years.

Evidence of sexual dimorphism, suggested by differences in the length-weight ($p < 0.05$) and weight-girth ($p < 0.01$) relationships (Table 2.2), as well as observed difference in relative frequencies by mesh size (figure 2.5 and 2.6) indicate that the selection properties for male and female spotted seatrout may also be different. The likelihood ratio test (Mendenhall et al. 1986) indicates a statistically significant difference in model parameter estimates by sex ($p<0.01$), and the modeling procedure was conducted by sex for the different years, as well as years combined. Table 2.3 gives model parameter estimates for the different years by sex along with asymptotic standard errors and model r^2.

Treating the sexes separately resulted in more consistent model parameter estimates across years for the females, especially those parameters related to the optimum selection length and standard deviation (table 2.3). Less consistency was observed for the males over the years, as only the optimum selection length seem to exhibit some stability. A number of parameter estimates for the males were not found to be significantly different from zero ($p < 0.05$), especially in 1990, in contrast to the females which were all found to differ from zero. Comparatively, generally poorer fits to the observed data were found for both males and females in 1990, which may result from low catches, particularly for male spotted seatrout in that year. Better fits to the

Table 2.3. Comparison of model selection parameter estimates by year and years combined (time-averaged model) for male and female spotted seatrout from gillnet data between 1988 and 1990. Also included are asymptotic standard errors and model r^2.

	1988	1989	1990	Combined	1988	1989	1990	Combined
Parameter	Coefficient (Asymptotic standard error)							
	Female				Male			
μ_0	8.410(0.512)	7.683(0.574)	6.446(0.857)	7.955(0.399)	10.019(0.710)	7.352(0.934)	6.446(0.857)	9.905(0.596)
μ_1	9.632(0.187)	10.047(0.207)	10.706(0.320)	9.885(0.143)	8.243(0.284)	9.705(0.372)	10.706(0.320)	8.363(0.237)
s_0	10.868(1.309)	11.747(1.256)	9.699(2.380)	12.189(1.172)	14.472(2.072)	23.085(2.175)	9.699(2.382)	18.426(1.559)
s_1	-6.306(0.949)	-6.505(0.885)	-5.324(1.753)	-7.062(0.842)	-10.453(1.625)	-16.617(1.675)	-5.324(1.753)	-13.125(1.174)
s_2	1.266(0.166)	1.273(0.152)	1.108(0.309)	1.381(0.146)	2.243(0.306)	3.351(0.321)	1.108(0.309)	2.675(0.216)
q_0	-9.169(1.375)	-1.470(1.296)	-13.743(2.195)	-6.041(1.207)	-23.708(2.897)	-14.037(3.041)	-13.747(2.196)	-5.897(1.174)
q_1	7.393(0.933)	1.993(0.868)	11.018(1.494)	5.170(0.825)	18.384(2.072)	11.474(2.172)	11.019(1.494)	5.459(1.202)
q_2	-1.305(0.152)	-0.381(0.141)	-1.976(0.247)	-0.917(0.135)	-3.347(0.358)	-2.059(0.371)	-1.976(0.247)	-1.082(0.198)
r^2	0.94	0.93	0.87	0.96	0.86	0.88	0.80	0.93

data were obtained when pooling the data over years for the different sexes. Model r^2 values were better than those obtained by fitting for years separately for both male and female spotted seatrout, and many of the parameter estimates had smaller standard errors.

Using the predicted model parameter estimates, selectivity curves were generated for the sexes separately and combined and are compared in figure 2.7. All three sets of curves shown in this graph represent model parameter estimates obtained by pooling data across years to illustrate the differences in the probabilities of capture between the sexes. The optimum selection lengths (peaks of the curves) for the various meshes occur at slightly greater sizes for the females than the males. Further, the females exhibit a slightly larger selection range for most of the meshes than the males and each curves has in general more positive skew.

Population Size Composition

A composite of the relative abundance estimates for the various sizes in the seatrout population gives a picture of the stock's size structure for a particular fishing year. The size structure of a stock is rarely static, but rather changes due to influences in recruitment and mortality through time brought about by variable environmental and exploitation patterns. Our estimates of relative abundance of the size-classes of fish should demonstrate the sort of dynamical change that recruitment and mortality have on the spotted seatrout population size structure. Figures 2.8 through 2.10, showing the seatrout population size structures for sexes separate and combined, should provide

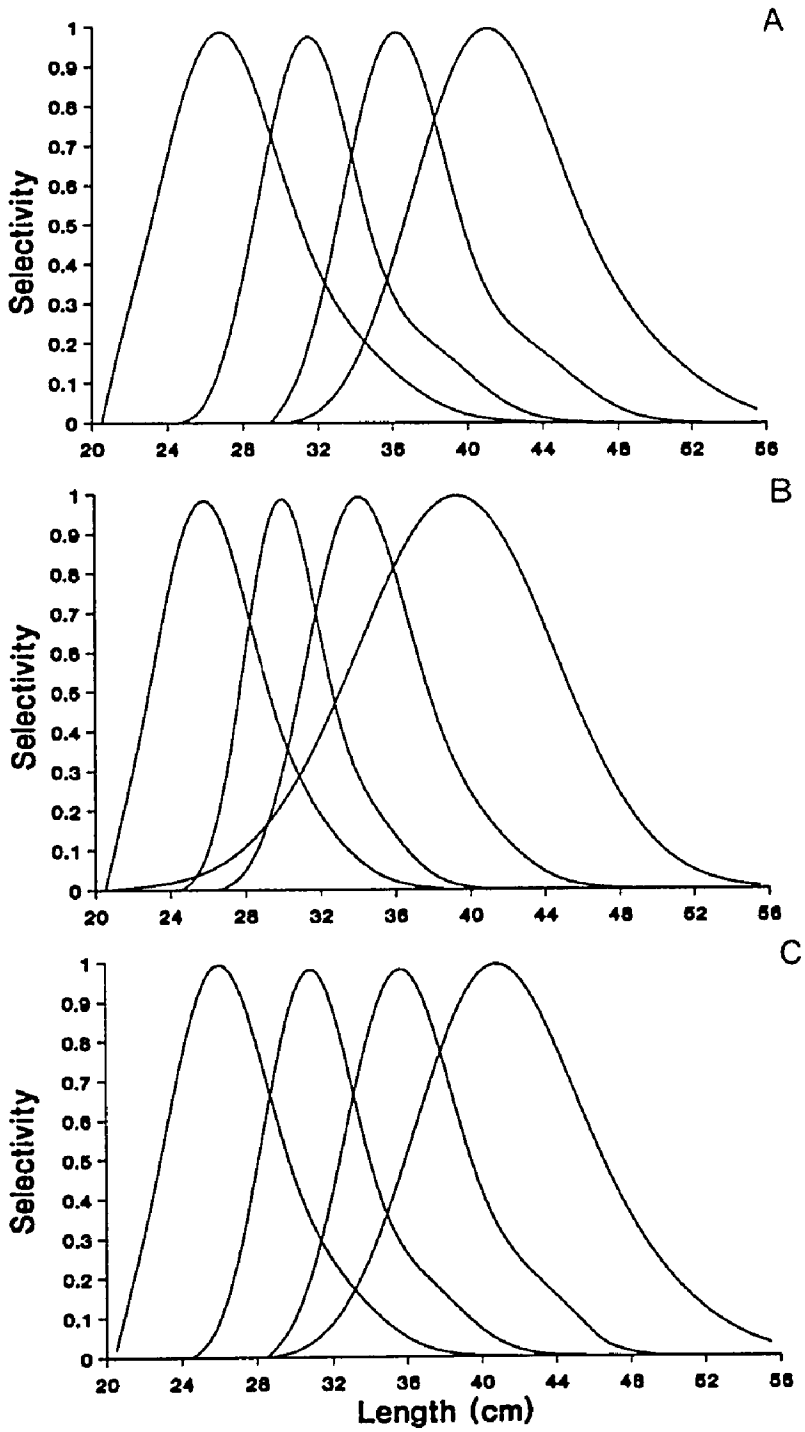

Figure 2.7. Comparison of the estimated selectivity for spotted seatrout caught in the various meshes showing curves for the a) females, b) males, and c) sexes combined. Curves shown were computed from time-averaged model to illustrate differences in the probability of capture between sexes.

information concerning recruitment and mortality. Two things are evident from these figures. First, the sexes appear to become differentially recruited by size, with the recruitment of female spotted seatrout into the fishable population delayed relative to males; and second, there appears to be a decline in relative abundance over most of the newly recruited and fully recruited size-classes for both sexes from 1988 to 1990.

Examination of the 1988 size structures for female and male spotted seatrout in figures 2.9 and 2.10, illustrate the differential recruitment at size patterns between the sexes. Here, female fish are only partially recruited below 31.5 cm where relative abundance estimates gradually increase (figure 2.9). Female spotted seatrout appear to become fully recruited by approximately 31.5 cm with relative abundance estimates remaining comparatively high until about 36.6 cm where a sharp decline in abundance is observed until 41.5 cm. In comparison, the 1988 size structure for male spotted seatrout (figure 2.10) suggest that fish become fully recruited by 27.5 cm while a partial recruitment pattern similar to the females is observed prior to that size-class. For males, relative abundance estimates remain comparatively high until 31.5 cm where a steep decline in abundance to 37.5 cm is observed. Comparison of these graphs suggest that recruitment by size for female spotted seatrout is delayed slightly and that once fully recruited into the fishable population remain more abundant than males.

The population size structures (figures 2.8 through 2.10) suggest that both female and male spotted seatrout recruit gradually into the

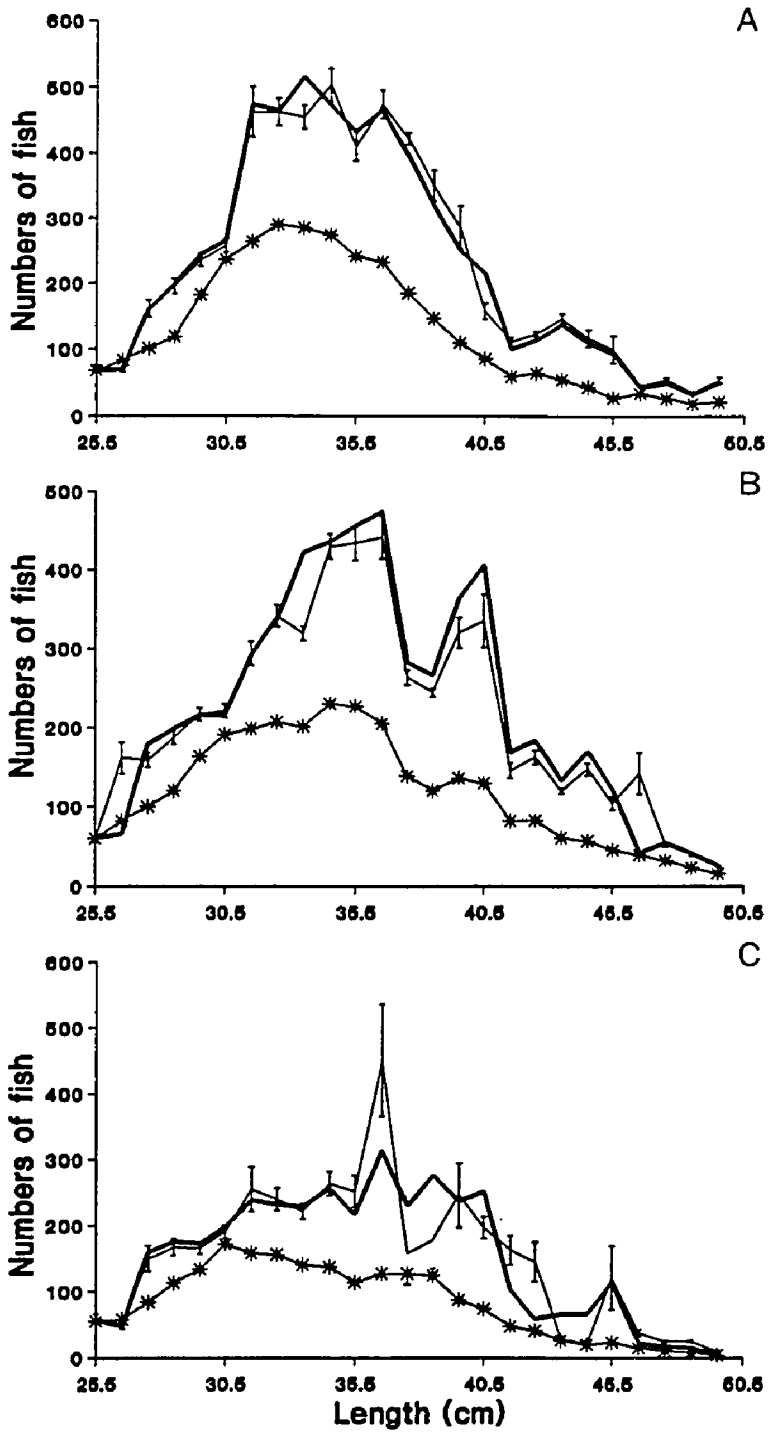

Figure 2.8. Shows the estimated seatrout population size compositions for sexes combined from a) 1988, b) 1989, and c) 1990. Estimates of relative abundance along with 95% confidence intervals (derived for year-specific model selection parameters) are shown as the light solid lines. Estimates from time-averaged models are shown as the dark solid lines and actual gillnet catches are given as stars.

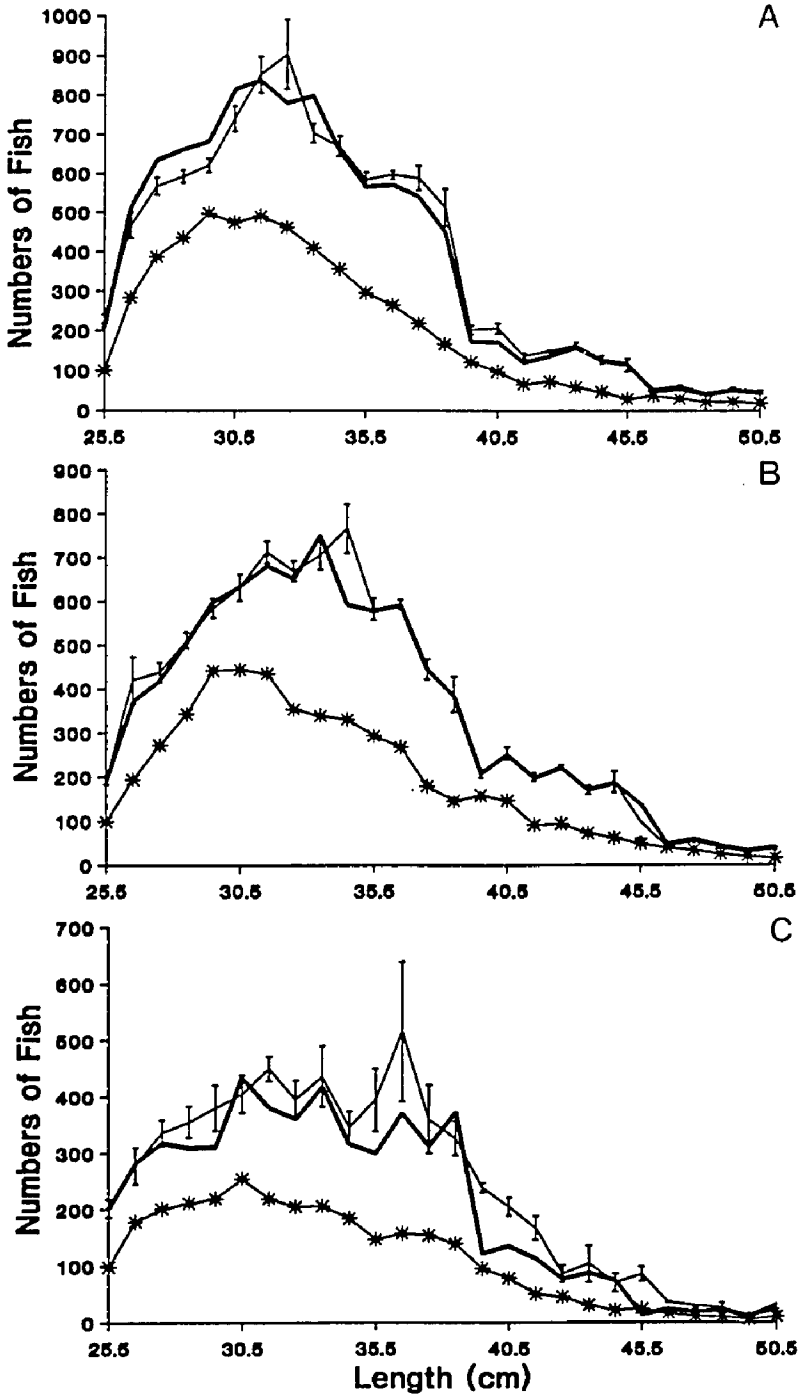

Figure 2.9. Shows the estimated population size compositions for female seatrout from a) 1988, b) 1989, and c) 1990. Estimates of relative abundance along with 95% confidence intervals (derived for year-specific model selection parameters) are shown as the light solid lines. Estimates from time-averaged models are shown as the dark solid lines and actual gillnet catches are given as stars.

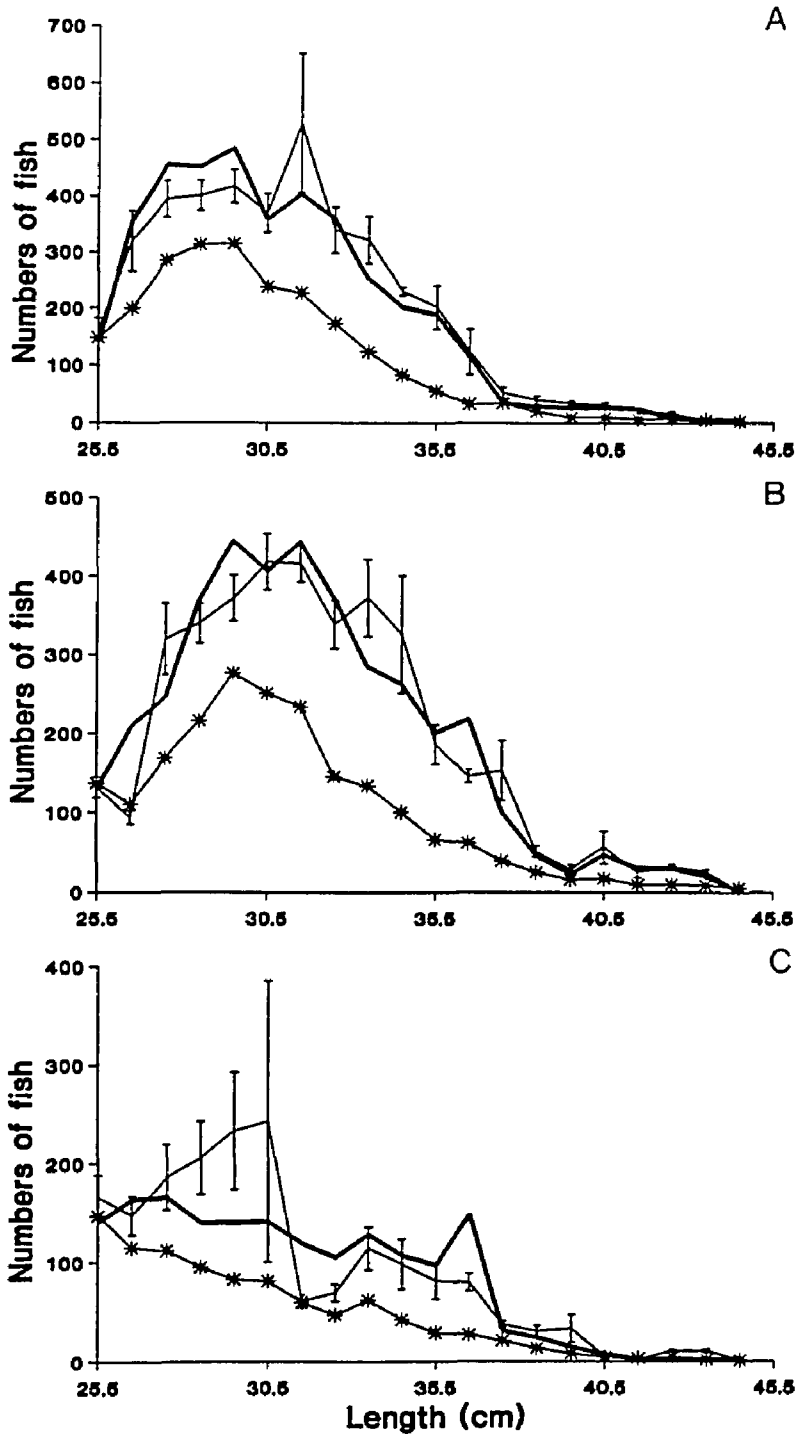

Figure 2.10. Shows the estimated population size compositions for male seatrout from a) 1988, b) 1989, and c) 1990. Estimates of relative abundance along with 95% confidence intervals (derived for year-specific model selection parameters) are shown as the light solid lines. Estimates from time-averaged models are shown as the dark solid lines and actual gillnet catches are given as stars.

gear and/or fishing grounds, where the vulnerability of an individual fish increases with size. Increased vulnerability with size may be due to the size selectivity of the fishing gear or a change in behavior or spatial distribution. The differential recruitment at size patterns between male and female spotted seatrout seen in these figures may be for the most part due to distributional differences related to spawning activity. Helser (1991 in review) found that when fish are forming spawning aggregations between May and August in the lower bays and beaches of the coastal zone, female seatrout are generally older and larger than males, which reach maturity quicker. The smaller females, which remain in the upper marsh areas during this time, may represent the partially recruited fraction of fish seen as the ascending limb of the 1988 curve in figure 2.9 and be responsible for the delay in recruitment to the fishable population in comparison to male seatrout.

It should be noted that the estimated 1988 seatrout population size composition shown in figure 2.8 appears slightly different from that of figure 4 in Helser et al. (1991). Differences in the population size compositions reflect the several modifications to the approach presented in this paper. The change in the model equation itself was shown to result in a slightly different set of parameter estimates which would naturally give rise to different capture probabilities for a given size-class of fish in a given mesh size. Additionally, omitting capture probabilities less than 0.10 which were done to standardize the estimation of relative abundances probably gave rise to slightly smaller estimates than previously obtained.

Subsequent to 1988, the population size structures exhibit a similar differential recruitment at size pattern between the sexes, however, changes in the entire stock's size composition are evident. Such changes in the stock's structure are observed here as reductions in the estimated relative abundances of newly recruited females (31.5 cm) and males (27.5 cm) from 1989 to 1990, along with a depression of abundances in 1990 over most of the fully recruited size-classes. For instance, relative abundances of females in the 31.5 cm size-class gradually decline from a high of approximately 800 fish in 1988-1989 to a low of about 400 fish in 1990. Further, larger sized females (33.5 cm to 38.5 cm) which were comparatively equal in 1988 and 1989 are depressed in 1990. A similar pattern of a gradual reduction in relative abundance estimates for male seatrout between 1988-1989 and 1990 in the newly recruited size-classes (25.5 cm to 27.5 cm) is also apparent in figure 2.10, although reductions in abundance are comparatively less for females. The male population size structure for 1990 (figure 2.10) does, however, indicate a similar depression of abundance over most of the fully recruited size-class.

It is unclear why such extreme changes are observed in the seatrout population size structure from 1988 to 1990. A minimum size restriction of 30 cm (12 inches) imposed on the fishery in 1987 might affect the size compositions by shifting the population size structures to larger sizes of fish. However, the observed depression of abundances in various pre- and post-recruit size-classes of fish for both sexes, seen in the 1990 population size structures may suggest another mechanism. A possible explanation for these patterns (figures 2.8

through 2.10), if one assumes that fish are not leaving the sampled area, is that the seatrout population may have experienced a decline in juvenile and pre-recruit abundance in 1989 due to a severe freeze that winter. The 1988 and 1989 size structures shown in these graphs represent data obtained prior to the December freeze, and therefore do not reflect those effects. However, such effects on recruitment may be seen in these figures as a decline over the size-classes where fish are becoming fully recruited in 1990 as they grow into larger sizes. It is also possible that the observed patterns in abundance are the result of both the combined effects of the severe freeze and changing distribution patterns. The declining relative abundances noted in these figures may be responsible for the increase in condition of fish from 1988 to 1990 shown in table 2.2, and represent a response of the seatrout population to density-dependent compensatory mechanisms (Ricker 1975).

If the estimated size compositions are representative of the seatrout population, then there are implications for the management of this stock. The Louisiana Department of Wildlife and Fisheries (LDWF 1991) has estimate the levels of spawning stock biomass per recruit (SSBR) for spotted seatrout in Louisiana through 1988. The average SSBR level for 1980's was near 15% and was adopted by the state as the conservation standard for this stock. It may be likely that stocks fished to excessively low SSBR levels have the propensity to experience recruitment failure brought about by environmental driving forces, although a minimum level may not be defined for most stocks of fish. For spotted seatrout, a minimum threshold level has not yet been defined nor is it certain whether current SSBR levels are adequate to ensure

maintenance of the stock. Given the current rate of exploitation on the spotted seatrout population and the possible effect that the 1989 freeze has had on the seatrout population size structure, estimates of the 1990 and 1991 SSBR may reveal whether the adopted conservation standard (15% SSBR) is adequate to sustain this stock at a biologically rational level in the face of uncertain environmental variability.

Variances of Relative Abundance Estimates

Examination of relative abundance estimates for the various size-classes of fish points to a seatrout population size structure which is dynamic through time and probably greatly affected by changing recruitment and mortality patterns. Estimates of relative abundance, which give rise to the size composition of the stock, are crucial to estimating other population quantities, such as mortality, as well as assessing the effects of management options. Therefore, it is desirable to estimate confidence intervals associated with the relative abundance estimates so that some degree of reliability can be advised in management decisions. Confidence intervals, constructed from estimates of size-class variance, were place about our estimates of relative abundance to assess the variability of those quantities.

The size compositions for the spotted seatrout population between 1988 and 1990, shown in figures 2.8 through 2.10, which include confidence intervals indicate that, in general, precision associated with relative abundance estimates are good. An exception to this generalization, however, occurs for male spotted seatrout in 1990. Variation associated with estimates of relative abundance can be

described in terms of three components: 1) within year variability over the different size-classes of fish; 2) interannual variation or the variation associated with the various size-class of fish from one year to the next; and 3) a mixture of the first two components between male and female fish.

The within year variability in relative abundance estimates appears to be the smallest of the three components. Excluding estimates for male fish in 1990, the worst case of within year variation is illustrated for male fish in 1988 of figure 2.10. Here, the largest confidence interval for this population size composition occurs at 31.5 cm, and estimates of relative abundance range from 400 fish to 650 fish. Confidence intervals associated with other size-classes in this size composition can be quite small, particularly for size-classes with comparatively small estimates of relative abundances. However, confidence intervals appear fairly consistent over those size-classes where relative abundance estimates are generally larger. The smallest case of within year variation is seen in the 1989 population size structure for the sexes combined (figure 2.8). Here, the variation in estimated relative abundances is not more than 100 fish for any given size-class and confidence intervals over the various sizes are rather consistent.

Interannual variation appears to be a more significant component of the variability in estimates of relative abundance than within year variance. Here, the variation in estimates of relative abundance over most of the various size-classes appear to increase in 1990 over the two earlier years for sexes combined (figure 2.8) as well as sexes separate

(figures 2.9 and 2.10). The population size compositions for male spotted seatrout, from 1988 to 1990, in particular illustrate more extreme interannual variation in abundance estimates. An interesting point to note is that estimates of relative abundance derived from the time-averaged model (years combined) fall with or are very close to 95% confidence intervals of the year-specific models over most size-classes for a given population size structure. The estimates from the time-average models give the expected relative abundances of the data averaged through time, and departures between estimates indicate deviations in the gillnet catches (and thus relative abundances) for a given size-class from what would occur on the average. This can, for instance, be examined for a number of different size-classes in the 1990 population size structures which suggest that gillnet catches (and thus size compositions) differ markedly from the two earlier years. This difference is most pronounced in the male spotted seatrout population size structure shown in figure 2.10. The fairly close agreement between estimates of relative abundances derived from time-averaged and year-specific models does, however, suggest that the relative accuracy in estimating the population size compositions is consistent.

Much of the within year and interannual variability in the estimates of size-class relative abundance are driven by the model's ability of fit the observed data. Table 2.1 indicates that the 1990 data for sexes combined produced relatively poorer model fits than the two earlier years. A similar situation is observed in table 2.3 where sexes are fit separately, although female data fit relatively better than the males for the 1990 data when separated. The increased annual

variation seen in the 1990 abundance estimates possibly reflect a change in the seatrout population size structure which may be the result of changing recruitment trends and increased natural mortality on pre-recruits. The effect of these changing patterns is seen as very different catch patterns (figures 2.8 through 2.10) which effect to a large extent the fit of the model, and is ultimately translated into increased variability associated with the estimates of relative abundance.

Fish populations are extremely dynamic and that changes in size compositions are a natural fact of life which many population-level models try to ignore. Interannual variation in population size compositions probably reflect changing trends in recruitment, natural mortality, and exploitation. Thus the ability to examine these effects on a fish population is essential to the understanding of the stock's dynamics and the biologically rational exploitation of the species. Here we present a model capable of estimating the population size composition of a fish stock and illustrate its utility as an integral part of a monitoring program. We further extend the novelty of this approach by developing a variance estimation procedure to derive confidence intervals about relative abundance estimates.

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CHAPTER III

Distribution of Abundance and Variations in the Size Composition of the Spotted Seatrout (*Cynoscion nebulosus*) Population in Coastal Louisiana

Introduction

Spotted seatrout (*Cynoscion nebulosus*) is one of four species of the genus *Cynoscion* which occur in the Gulf of Mexico (Weinstein and Yerger 1976) but whose range extends as far north as Cape Cod, Massachusetts and as far south as the lower Gulf of Campeche, Mexico (Tabb 1976). Spotted seatrout are generally found to be most abundant in Gulf of Mexico from Florida's West coast to Texas (Iverson and Moffet 1962; Tabb 1966; Merriner 1980). Despite this relatively large geographic range, the adult spotted seatrout is a non-migratory species whose functional home range may be restricted to specific estuarine systems (Iverson and Tabb 1962; Arnoldi 1984) and form subpopulations which remain distinct due to the relative isolation of estuaries, particularly along the northeastern Gulf of Mexico (Iverson and Tabb 1962; Perret et al. 1971; Weinstein and Yerger 1976). Although there are a number of conflicting conclusions concerning subpopulations of spotted seatrout along the coastal estuarine systems of the Gulf of Mexico (Weinstein and Yerger 1976; Ramsey and Wakeman 1987; King and Pate 1988), numerous studies suggest that seatrout at least show different population characteristics in terms of growth and morphometries between different estuarine systems (Wakemen and Ramsey 1985; Colura and King 1989; Weiting 1989).

The distribution of spotted seatrout abundance within a given estuarine system is related to various biotic and/or abiotic factors, although these may vary from one estuary to the next. Distributions of spotted seatrout in Florida estuaries were identified with a number of important determinants which included areas of quite, brackish water and extensive submergent vegetation with adjacent deeper "holes" (Tabb 1959). Tabb (1966) also suggested that adult spotted seatrout are most commonly found in brackish non-tidal inner bays and lagoons and Gilmore (1977) indicated seatrout abundance was associated with grass flats and sand bottoms. Similar associations between seatrout occurrence and habitat type can also be documented in Alabama, Mississippi, and Texas (Pearson 1929; Miles 1950; Tabb 1958; Lorio and Perret 1980; Zieman 1982; Mercer 1984). In many of the estuaries of Texas and Louisiana, adult spotted seatrout prefer habitat near sandy bottoms or shell reefs, around submerged or emergent islands, and within the deep bayous and canals in the inshore areas of the Gulf of Mexico (Lorio and Perret 1980; Hoese and Moore 1977).

Although much is known about the habitat preferences of spotted seatrout within the estuaries of the northern Gulf of Mexico, little information relevant to management of the species is available which addresses size/age/sex specific distributions of abundance over larger spatiotemporal scales, such as intraestuarine zones over seasons. Available information on the distributional ecology of spotted seatrout suggests that seatrout abundance does vary over wider spatiotemporal scales and that the life history stage may be an important factor affecting the pattern of distribution. One study in coastal Louisiana,

implementing experimental gillnets in conjunction with tagging, suggested that most of the seatrout population appears en masse in Lake Calcasieu in the spring and fall (Arnoldi 1984). Arnoldi (1984) reports gillnet catch rates of spotted seatrout for four different mesh sizes as an indicator of adult size composition but does not present evidence to suggest differential patterns of size-class (or life history stage) abundance on any spatiotemporal scale. A more recent and comprehensive estuarine inventory program for the Central Gulf of Mexico estuaries has compiled and characterized the distribution and abundance of many estuarine fish species, including among them spotted seatrout (Czapla et al. 1991). These authors examine spatial abundances over broad salinity scales defined as tidal fresh (0.0-0.5 ppt), mixing (0.5-25.0 ppt), and seawater (>25.5 ppt). Although this study provides spatial and temporal comparisons of spotted seatrout abundance (based on catch rates) in a number of Louisiana's estuaries, it lacks a rigorous statistical examination.

Numerous observations indicate that estuarine species of fish are not evenly distributed across estuarine salinity gradients (Segerstale 1959, Remane and Schlieper 1971) and recently multivariate statistical techniques have been applied to analyze the community structure across environmental gradients (Digby and Kempton 1987). Such multivariate statistical approaches may prove useful for the analysis of the distributional ecology of a single species as well, because individuals of a given species may seek different optimal habitats along

environmental gradients, both spatially and temporally, depending on the life history stage or other factors (Deegan and Thompson 1985; Ross and Epperly 1985).

In this paper we use a number of multivariate statistical techniques to examine the distributional ecology of the spotted seatrout populations in four different estuarine systems in coastal Louisiana. We analyze three years (1988 to 1990) of experimental gillnet catch data on spotted seatrout from over 28 stations sampled in various habitats and attempt to answer the following questions. 1) Can the stations sampled over the various spotted seatrout habitats be classified into "natural" groupings based on their physical characteristics. 2) If such environmental zones exist, is the abundance of spotted seatrout statistically associated with them both in time and space. 3) Do abundance patters over the spatiotemporal scales investigated depend on life history stage of the individuals in the population. And 4) what are the management implications of the distributional ecology of spotted seatrout.

Study Area

In response to concerns about its estuarine fishery resources, the state of Louisiana initiated a coast-wide finfish monitoring program which partitioned its coastal zone into seven primary hydrographic study units. In each hydrographic study area stations were chosen from among various habitats extending from the low salinity, brackish marshes to higher salinity, beaches and lower bays of the Louisiana coastal zone. At least two transects were established in each of the hydrographic

areas. The transects were designed to cover some of the various spotted seatrout habitats and salinity regimes typical of the estuaries in Louisiana. Stations were sampled twice monthly using a five panel experimental gillnet. Hydrological data was also collected at each station when an experimental gillnet set was made and included salinity (ppt), water temperature, water turbidity (measure with secchi disk), and sea state (ft).

For this analysis, We chose only those stations within the various hydrographic study areas for which adequate catches of spotted seatrout and sampling coverage (i.e not more than two consecutive months were no gillnet sets were made) were obtained. Thus, due to the relatively low catches of seatrout in the experimental gillnets over most of the stations in hydrographic areas 6 and 7 (west of the Atchafalaya Bay) these were exclude. All other study areas, from Breton sound to the Atchafalaya Bay (Areas 1 through 5), were retained due to a sufficient number of stations along the transects within these systems. Therefore, in this paper we consider four estuarine systems of the Mississippi River deltaic plain covering the eastern portion of Louisiana's coastal zone. Spotted seatrout catches from the estuarine systems used in this analysis comprised over 90% of the total annual gillnet catches. The estuarine systems remaining and the number of stations within each used in the analysis were: Breton Sound (Areas 1 and 2) with 10 stations; Barataria Bay (Area 3) with 5 stations; Terrebone Bay (Area 4) with 6 stations; and Caillou Bay (Area 5) with 7 stations. Figure 3.1 shows the

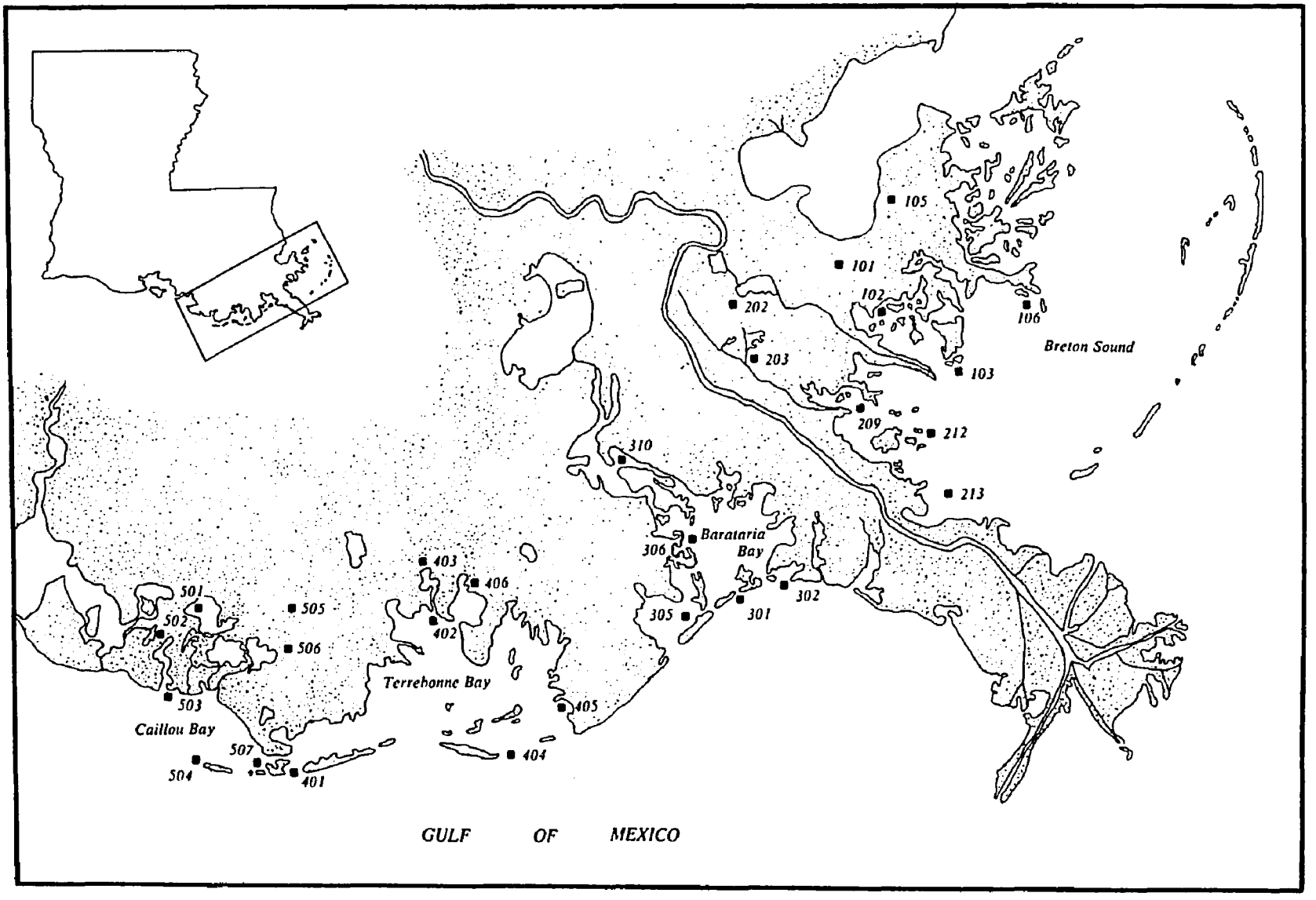

Figure 3.1. Study area over the eastern portion of Louisiana's coastal zone.

Table 3.1. Stations sampled in four estuarine systems of coastal Louisiana giving 25th percentile of salinity (ppt) and the estuarine zone to which the station was classified based on the results of clustering procedure. U=upper zone (0-9 ppt), I=intermediate zone (10-14 ppt), and L=lower zone (15-30 ppt).

ESTUARINE BASIN SYSTEM	STATION	LATITUDE	LONGITUDE	ESTUARINE ZONE	25th PERCENTILE OF SALINITY (ppt) 1988	1989	1990
BRETON SOUND (Area 1)	105	29 50 00	89 31 00	I, U-90	10.6	9.9	8.8
	101	29 48 30	89 40 00	I, U-90	11.0	10.6	7.8
	102	29 44 00	89 36 00	I, U-90	11.0	11.5	7.9
	106	29 44 30	89 22 00	L, I-90	18.0	15.7	13.8
	103	29 40 30	89 26 30	L, I-90	18.5	15.0	11.7
(Area 2)	202	29 45 42	89 49 00	U	6.2	8.1	4.2
	203	29 42 24	89 53 18	U	4.2	5.1	2.9
	209	29 36 42	89 41 30	I, U-90	10.7	9.9	7.7
	212	29 37 42	89 35 42	I, U-90	13.5	11.2	7.8
	213	29 37 42	89 35 42	L, I-90	17.7	12.8	9.6
BARATARIA BAY (Area 3)	310	29 31 10	90 08 75	U	1.0	3.8	3.0
	306	29 21 25	89 59 30	L	15.0	15.5	15.0
	305	29 20 20	90 06 20	L	17.0	17.3	14.8
	301	29 17 50	89 55 25	L	20.0	20.0	17.0
	302	29 15 00	89 57 50	L	20.0	20.3	17.0
TERREBONNE BAY (Area 4)	403	29 25 45	90 31 25	U	6.8	6.0	4.5
	406	29 22 05	90 17 55	I, L-89	13.3	16.7	13.1
	402	29 17 47	90 23 30	L	19.6	16.0	15.7
	405	29 10 00	90 17 24	L	22.1	21.2	20.2
	404	29 05 18	90 13 37	L	29.2	19.9	22.5
	401	29 02 30	90 47 48	L	27.6	22.3	22.2
CAILLOU BAY (Area 5)	501	29 20 36	90 57 30	U	3.9	1.2	0.8
	505	29 20 29	90 45 18	U	2.3	1.3	1.2
	506	29 15 35	90 47 36	U	5.5	4.8	3.9
	502	29 15 12	90 02 27	U	6.5	3.5	3.1
	503	29 10 41	91 01 48	L, I-90	17.3	15.4	13.3
	504	29 03 40	90 57 38	L	23.2	23.7	21.1
	507	29 02 11	90 49 24	L	23.7	20.6	20.2

positions of the sampled stations in each of the basin systems of coastal Louisiana under investigation and Table 3.1 gives the latitude and longitude of each station.

Materials and Methods

Sampling and Gillnet Data

State biologists employed a "run-around" method to capture spotted seatrout in monofilament nylon experimental gillnets in one of five possible mesh sizes: 2.0, 2.5. 3.0. 3.5, and 4.0 in. (5.08, 6.35, 7.62, 8.89, and 10.16 cm, respectively) stretch measure. At each station, experimental gillnets, measuring 750 ft (228.6m) in length (150 ft per mesh panel), were deployed by biologist and encircled approximately three times by the fishing vessels to drive fish into the nets. The nets were then retrieved, starting with the panel first entering the water, and the catch of spotted seatrout enumerated by mesh. Fish were measured to the nearest millimeter, weighed the to the nearest ounce, and examined for sex and maturity stage. Fish were staged for maturity in the field by gross examination of the gonads and given the following grade based upon the biologist's observations: 1-immature; 2-newly maturing or well recovered spent fish; 3-fat storage absorption and ripening stage; 4-ripe running; and 5-spent fish. Readers interested in additional information concerning the equipment and method of capture used should consult Adkins and Bourgeois (1982).

Gillnets of a single mesh are highly size selective. The entire gang of meshes in the experimental gillnet should, therefore, sample

over a fairly large portion of the size composition of the population (Helser et al 1991). Gillnet selectivity studies for this gear configuration indicate different selection patterns for the male and female spotted seatrout and as a result differing optimum selection lengths for the various meshes (Helser et al. 1991a; Helser et al. 1991b). Table 3.2 gives the total lengths of male and female spotted seatrout most likely to be caught by the various sized meshes used in the experimental gillnet configuration. The largest mesh size (4.0 inch) was excluded due to the relatively low numbers of fish caught in that mesh. Also given in table 3.2 are the ages corresponding to the lengths as determined by Weiting (1989). These data indicate that the first panel (2.0 inch mesh) should capture with a high probability male and female spotted approximately a year and a half old (about 26 cm). The lower selection limit (50% probability of capture) of the 2.0 inch mesh for both male and female fish is 23 cm and represent new recruits which would have been spawned during the summer the previous year. The remaining larger meshes should sample with relatively high probability up to approx. 45 cm which corresponds to an age 3.6 and age 5 female and male seatrout, respectively (Table 3.2). Size-classes of seatrout beyond the lower (23 cm) and upper (45 cm) selection limits of this gear configuration are not effectively sampled. This analysis, therefore, restricts its inferences concerning the abundances of spotted seatrout within the specified size categories.

The index of abundance used for the various size categories of each sex in the seatrout population is the catch-per-unit effort specific to each mesh size. Effort was measured as the number of

Table 3.2. Lengths (cm) and ages (yrs.) of male and female seatrout most likely to be caught in the various mesh sizes used in the experimental gillnets. Expected length (age) are those sizes of seatrout which have the greatest probability of capture (100%) in the various meshes. Lower and upper lengths (age) are those sizes of seatrout which have a 50% probability of capture.

MESH SIZE (IN.)	OBSERVED MEAN LENGTH (cm)	ESTIMATED LENGTHS[a] (CM) AND AGES[b] (YRS.) LOWER LENGTH (AGE)	EXPECTED LENGTH (AGE)	UPPER LENGTH(AGE)
		Female Seatrout		
$F_{2.0}$	29	23(1.0)	27(1.3)	31(1.6)
$F_{2.5}$	33	28(1.4)	31(1.6)	35(1.9)
$F_{3.0}$	37	33(1.7)	36(2.0)	40(2.3)
$F_{3.5}$	41	37(2.0)	41(2.4)	46(3.6)
		Male Seatrout		
$M_{2.0}$	28	23(1.1)	26(1.5)	29(1.8)
$M_{2.5}$	31	28(1.7)	30(2.0)	32(2.2)
$M_{3.0}$	35	31(2.1)	34(2.5)	38(3.2)
$M_{3.5}$	36	33(2.3)	39(3.4)	45(5.0)

[a] Estimated size selectivity for the various meshes used in the experimental gillnets (Helser et al. 1991).
[b] Estimated ages at size based on the growth equations of Weiting (1989).

gillnet sets within a given strata. Since the number of sets at a given station during a given month were unequal the total catch for station and month was divided by the number of sets to obtain an average monthly catch. The catch was then summed over the various spatial and temporal strata defining the basic unit of catch used in the analysis as, C_{ijkl}, or the catch of fish in mesh i of sex j in temporal strata k and at spatial strata l. The data were then logarithmic transformed, $\log_e(C_{ijkl})$, to approximate normality (Pennington 1983).

Spatiotemporal Scales

We used a hierarchical agglomerative clustering procedure (SAS 1985) to group stations with similar physical environments, based on salinity, turbidity, and sea state. We chose the 25^{th} quantile of these variables as input to the distance matrix since it reflects that a given station's observed physical variable occurred (i.e. salinity) above a certain value 75% of the time. The input data matrix for the various physical parameters was based on mahalanobus distance measures and the average linkage algorithm, which treats the distance between two clusters as the average distance between all pairs of items, was used as the assignment rule (Johnson and Wichern 1988). It was tempting to use standardized gillnet catches as an additional clustering variable, however, it was the purpose here to obtain meaningful "natural" groupings of stations based on similar abiotic factors a priori and then ascertain whether such environmental structures were related to the seatrout population characteristics, such as an abundance index (CPUE), size compositions, sex differences etc, over some temporal scale.

We chose the annual spawning cycle of spotted seatrout as a natural temporal scale. Spotted seatrout are described as a heterochronus spawners which mature continuously and sequentially release batches of eggs throughout a prolonged spawning season (Weiting 1989). The duration of the spawning season for seatrout in the northern Gulf of Mexico has been reported by a number of studies as April through September (Pearson 1929; Gunter 1945; Hein and Shepard 1979; Overstreet 1983; Brown-Peterson et al. 1988; Colura et al. 1988; Weiting 1989). Although lacking detailed histological examination the numbers of seatrout collected between 1988 and 1990 used in this study (approximately 17,000) may provide a good representation of the seasonal spawning cycle for the seatrout population. Figure 3.2 shows the percent contribution of each gonad condition index to the monthly total for both male and female seatrout. Fish which are observed to be a gonad condition index of 4 or greater represent those which will eminently spawn. Here, the graph suggests that for female spotted seatrout the most intense spawning activity begins in late April and continues through August. Thus, based on the above information we chose three separate time periods to represent the temporal scales used in the subsequent analysis: May-August (Spawning season); September-December (Post-spawning season); and January-April (Pre-spawning season).

Statistical Methods

We employed two multivariate statistical techniques to approach the second and third questions/objectives of our study. The first, Principal Components Analysis (PCA), was used on the covariance matrix

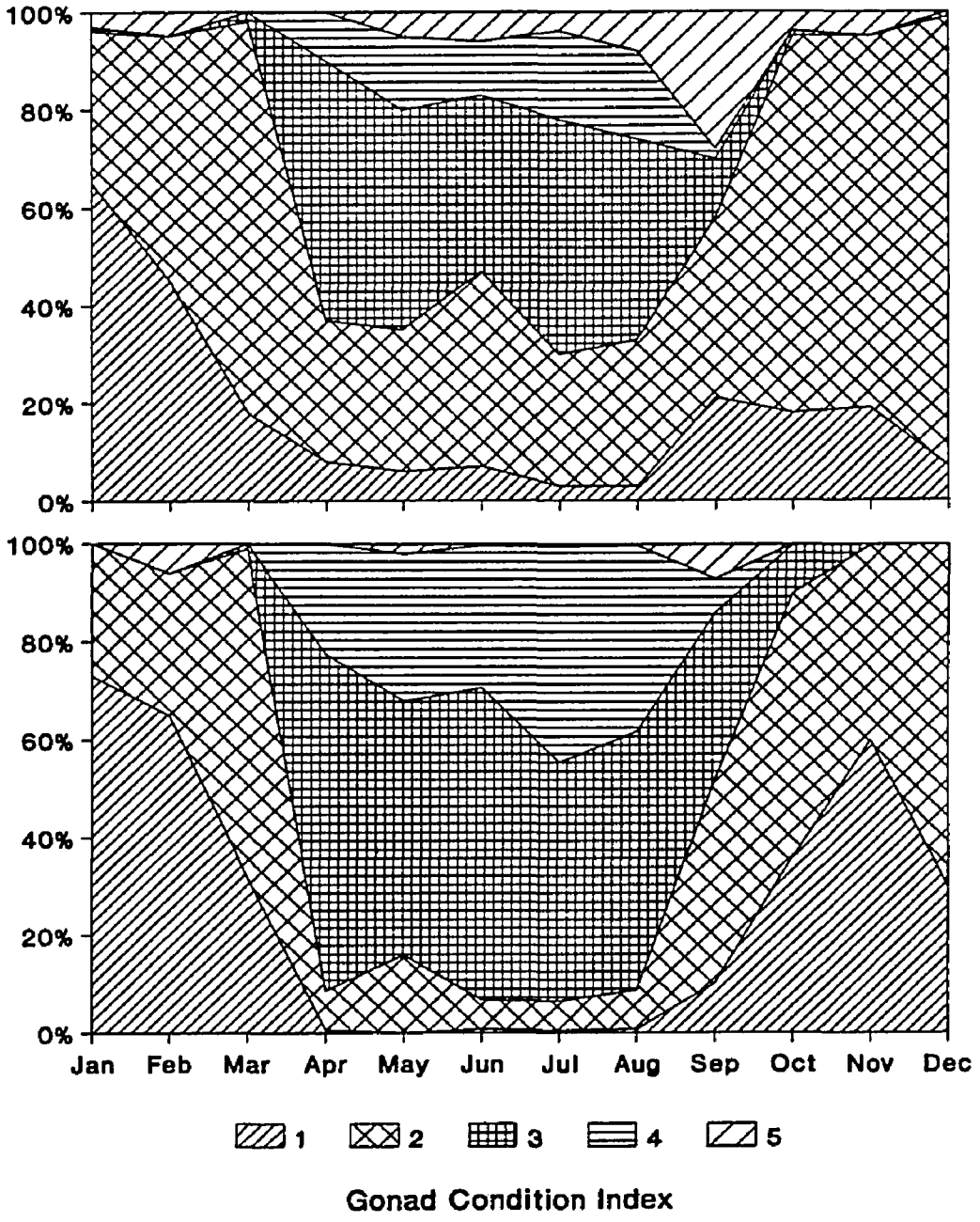

Figure 3.2. Percent contribution of the total seatrout caught by month identified with each gonad condition index for female (top) and male (bottom) fish separately.

of seatrout abundance by mesh size (size/age categories) as a data reduction technique and to reveal relationships in the covariance structure. PCA is a technique concerned with explaining the variance-covariance structure through a few orthogonal linear combinations of the original variables which represent new coordinate axes (Johnson and Wichern 1988). The new axes represent directions of maximum variability and it is through the examination of these new axes that interpretations of the variance-covariance structure can be achieved. Various orthogonal rotations, such as the varimax rotation, can be used to assist in structure interpretation (Johnson and Wichern 1988). We anticipated that this approach would prove particularly useful in identifying those mesh sizes (size/age categories of fish) which give rise to information concerning difference in the seatrout population size composition over the spatiotemporal scales. The relative abundance data (CPUE) for the various mesh sizes of seatrout were reduced to 2 principal components using the FACTOR procedure (SAS 1985). Factor loadings from the PC factor analysis were subjected to orthogonal factor rotation using the varimax rotation to enhance interpretation of the factors and derive rotated PC scores. The PC scores for the first two PC's for each observation were saved and output for subsequent general linear model analyses (GLM) for formal hypothesis testing. We conducted an Analysis of Variance on the first two rotated PC scores and on the actual CPUE data for the various meshes corresponding to those interpreted factors and tested of differences between years, estuarine basins, estuarine zones, seasons, and their interactions.

These data and additional methods were used to examine the spotted seatrout population size compositions on a continuous scale. Seatrout population size compositions were constructed from relative abundance estimates for the various size-classes of fish and compared over various spatiotemporal scales. Relative abundances of the various size-classes of fish in the population were computed from estimated gillnet selectivities for the various meshes by the method of Helser et al. (1991a). This approach calculates the numbers of fish of a given size-class which must have encountered the mesh of a given size in order to observed the actual catch, based on the estimated probability of capture. Helser et al. (1991b) provides a method of estimating variances for the estimates of relative abundance for the various size-classes which are used to compute 95% confidence intervals, a measure of uncertainty.

Results

Cluster Analysis

Results of the clustering procedure indicated that three "natural" groupings or clusters were formed out of 84 possibilities (28 stations x 3 years). Agglomerative hierarchical methods start with as many clusters as there are objects to be clustered (Johnson and Wichern 1988). Most of the variation in the covariance matrix for three clustering variables lies in a single dimension (98% of the variation) and salinity is probably most important variable of those measured in discriminating between groups. Our interpretation of these three

groupings are essentially salinity zones which correspond to upper, intermediate, and lower spatial positions within the estuarine system. The range of salinity values for the stations within each of these zones are between 0 to 9 ppt; 10 to 14 ppt; and 15 to 30 ppt for the upper, intermediate, and lower estuarine zones, respectively (Table 3.1).

Table 3.1 gives the salinity zone classification based on the clustering procedure for each station and year as well as observed values of the 25^{th} percentile of salinity. Stations in the Breton Sound region (east of the Mississippi river) generally lack an upper estuarine zone (Oligohaline zone) due to limited fresh water input from the Mississippi River which flows primarily westward, although in 1990 many stations were reclassified as upper estuarine zone (0-9 ppt). Numerous stations within the estuarine systems west of the river were classified as lower estuarine zones or polyhaline (15-30 ppt), however these systems generally lacked stations which could be classified as intermediate zones (10-14 ppt). Generally, lower salinities at stations in the upper reaches and relatively higher salinities at stations in the lower reaches of the estuarine systems west of the Mississippi River indicate that such systems receive substantial fresh water input but are also tidally influenced to a large extent.

The annual variation in mean salinities between the upper and lower estuarine salinity zones for each year and a three year average by month are shown in Figure 3.3. Mean salinities for stations classified as upper estuarine zone (low salinity stations) in 1990 appear to fall well below 95% confidence intervals of the three year average over most months from July through December. This aberrant salinity pattern is

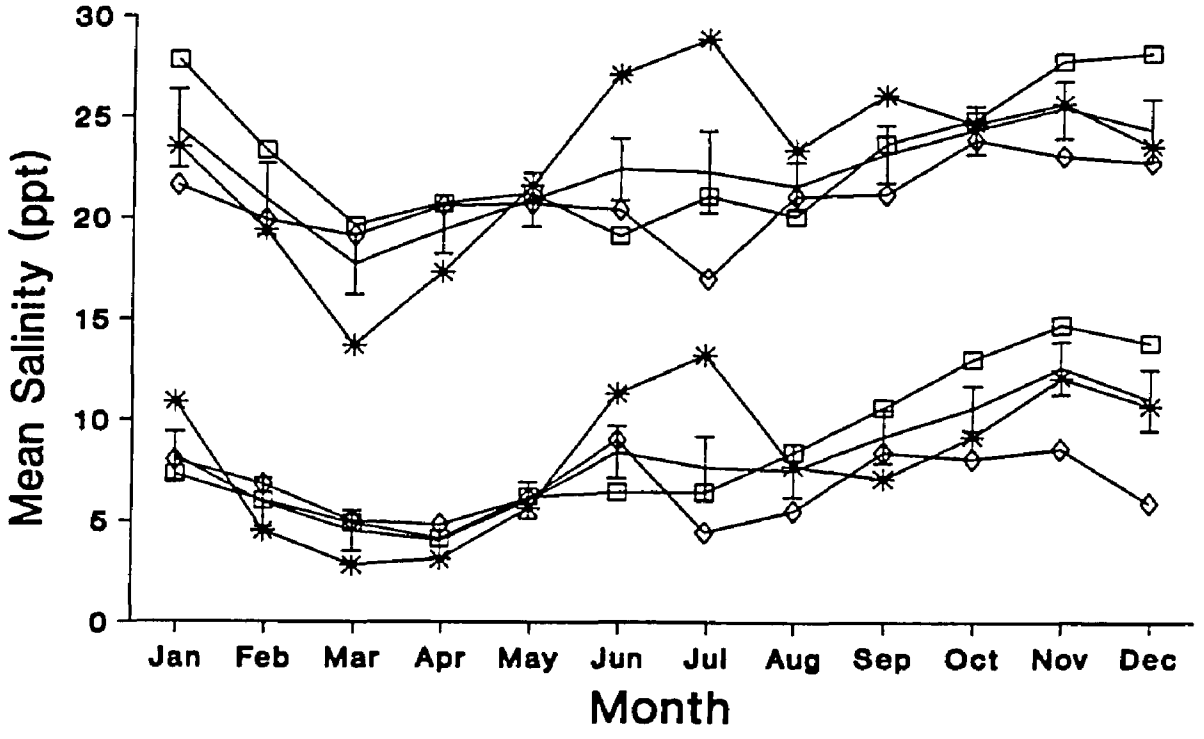

Figure 3.3. Annual variation in mean salinity for stations classified as upper (low salinity) and lower (high salinity) estuarine zones based on the cluster analysis for 1988 (star), 1989 (square), and 1990 (diamond). Salinity of the three-year average for each zone is shown with 95% confidence intervals.

probably the result of greater than average rainfall in Louisiana in 1990 and accounts for the re-classification of intermediate zone stations in areas 1 and 2 into the upper zone group in 1990 (table 3.1). The high degree of separation of mean salinities between the upper and lower zones shown in figure 3.3 suggests that stations sampled in this study do form "natural" groupings which fall into discrete positional zones within the estuarine system and exhibit distinct salinity ranges.

Principal Components Analysis

A two-factor PCA model explained 78% of the cumulative variance in the covariance matrix of the original data set with the first and second factor contributing 65% and 13%, respectively. Additional factors to analyze these data were not considered as eigenvalues beyond the first two were less than unity. Results of the PCA are given in table 3.3 along with unrotated and rotated factor loadings. The first factor appears to describe an overall abundance factor with relatively high positive loading from each mesh size category (Table 3.3). The second factor is bipolar and seems to differentiate between size categories with negative loadings on the smallest two mesh sizes (2.0 and 2.5) for the females and the smallest mesh size (2.0) for the males.

An orthogonal rotation (varimax rotation) of the original factor pattern was particularly useful for enhancing interpretation of the factors. The rotated factor pattern given in table 3.3 for the second factor reinforced our previously suggested interpretation of a size factor, particularly a large size seatrout. Here we see high positive loadings greater than 0.6 for the largest two meshes (3.0 and 3.5) for

Table 3.3. Results of principal components factor analysis on the spotted seatrout Log_e(CPUE) for the various meshes used in the experimental gillnets. Shown are the loadings for unrotated and rotated (varimax rotation) estimated factor patterns.

VARIABLE MESH SIZE	ESTIMATED FACTOR PATTERN		ROTATED ESTIMATED FACTOR PATTERN		COMMUNALITY ESTIMATES
	FACTOR 1	FACTOR 2	FACTOR 1	FACTOR 2	
$F_{2.0}$	0.7317	-0.5627	0.9188	0.0881	0.8520
$F_{2.5}$	0.8751	-0.3054	0.8479	0.3741	0.8590
$F_{3.0}$	0.9054	0.0284	0.6423	0.6387	0.8250
$F_{3.5}$	0.8050	0.1878	0.4601	0.6867	0.6833
$M_{2.0}$	0.8222	-0.2704	0.7855	0.3636	0.7500
$M_{2.5}$	0.8630	0.0915	0.5683	0.6596	0.7531
$M_{3.0}$	0.7833	0.3650	0.3233	0.8014	0.7468
$M_{3.5}$	0.6219	0.5780	0.0599	0.8470	0.7209
EIGENVALUE	5.190	0.999			
PROPORTION OF VARIANCE EXPLAINED	0.648	0.130			
CUMULATIVE VARIANCE EXPLAINED	0.648	0.778			

the females and largest three meshes (2.5, 3.0, 3.5) for males. The first factor (Table 3.3) which was initially interpreted as an overall abundance effect may also suggest a size factor based on the rotated factor pattern, however in this case a small size component as the smallest two meshes (2.0 and 2.5) for the females and the smallest mesh (2.0) for the males load relatively high. A dual interpretation for the first factor may not seem unreasonable since the catches of seatrout in those meshes with higher relative loadings (2.0 and 2.5 for females and 2.0 for males) account for numerically the greatest catches of all meshes. Communality estimates (table 3.3) indicate a fair to high correlations between the original set of response variables (size categories) and the two-factor PCA model.

The two-factor principal component solution accounts for much of the total (standardized) sample variance (78%). Since our sample is comprised of spatiotemporal (zones and season) subpopulations of data we can partition the total sample variance in relation to those spatiotemporal scales. Figure 3.4 shows the principal component scores (rotated) of the individual data points on the first two factor axes to display the sample variance over season. Here the plotted points for each season form an ellipsoid whose major axis lies in the direction of the first factor axis (a result giving a graphic display of the large eigenvalue corresponding to the first factor from the PCA). An important feature shown in figure 3.4 is the distinct and gradual separation of the data between the estuarine zones (upper vs. lower) which seems to begin during the pre-spawning season and is most compelling during the spawning season. The separation between data

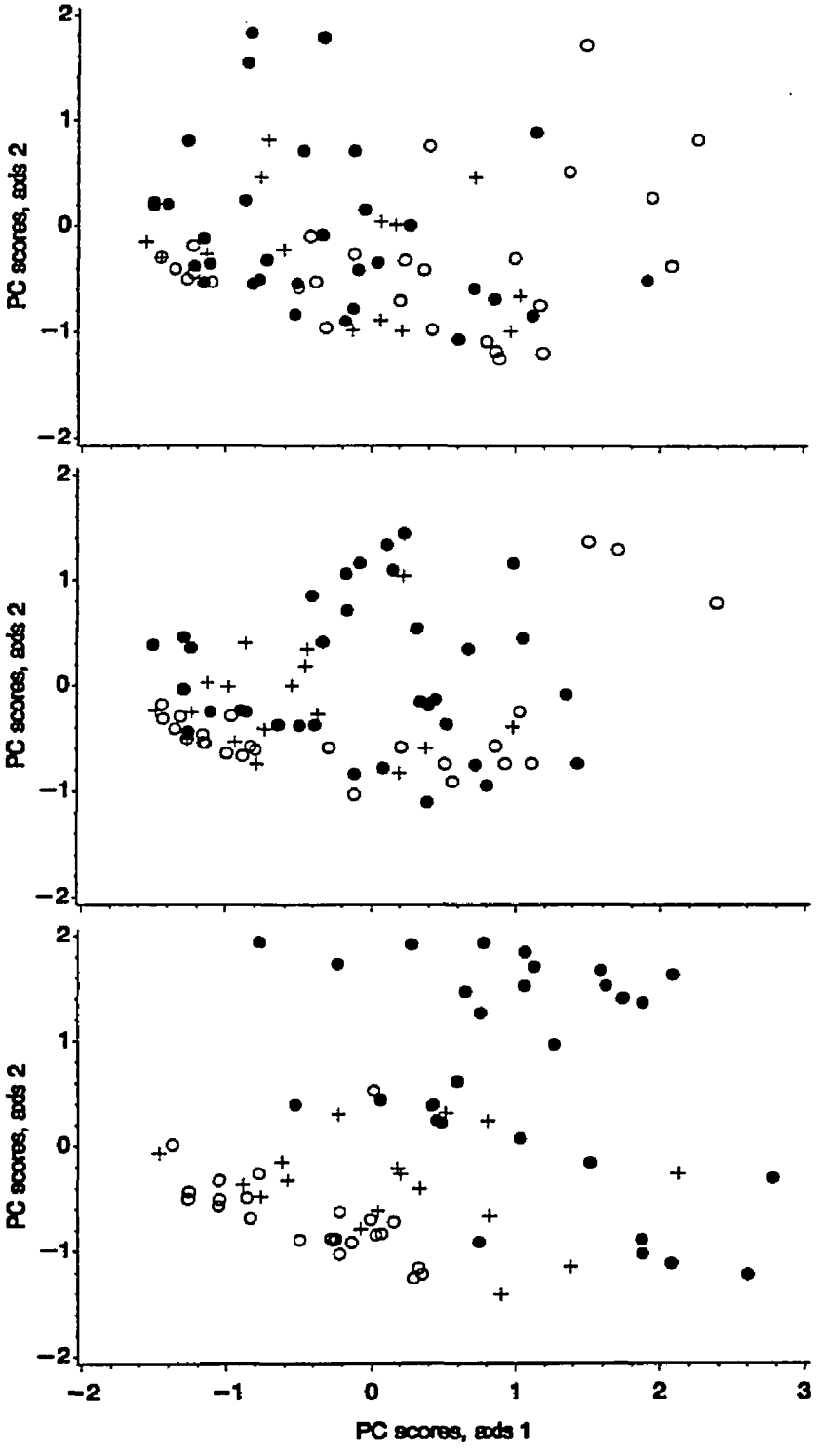

Figure 3.4. Shows the principal component scores (rotated) for the individual data points plotted on the first two PC factor axes over the various temporal and spatial scales. Estuarine zones are shown as open circles (upper), pluses (intermediate), and closed circles (lower) for the post-spawning (top), pre-spawning (middle), and spawning (bottom) seasons.

points associated with the upper and lower estuarine zones can be described by a linear discriminating function in relation to both axes, particularly axis 2 which appears to represent the larger sized fish component. What makes this result particularly interesting is that the zones, which were grouped from the cluster analysis (on the basis of physical variables) and independent of the catch data, are now clearly discriminated on the basis of the catch data (from the first two PC factors).

Evidence to further reinforce our initial interpretation of these factors are displayed in figures 3.5 and 3.6 where the actual catch data (abundance and size composition) are plotted on the PC scores for axes 1 and 2, respectively. Abundance (for both small and large sized fish categories) is measured as the sum of the Log_e(CPUE) for each mesh which loaded relatively high from the PC factors (Table 3.3, loadings > 0.7 and 0.6 for the first and second factors, respectively). A close linear relationship between these data and PC scores of axis 1 in figure 3.5 suggest a high degree of correlation between small fish abundance and the first factor axis. In general, the higher the PC scores of the individual data points the greater abundance. Similarly, figure 3.6, shows the relationship between the larger fish abundance (factor 2), as indexed by the ratio of small size to larger size fish abundance (ratio of 0 indicates unity), and the PC scores for the second factor. This close linear relationship also suggests a high correlation between the PC scores of axis 2 and large fish abundance. Plots in figures 3.5 and 3.6 are shown for both the post-spawning (Sept.-Dec.) and the spawning

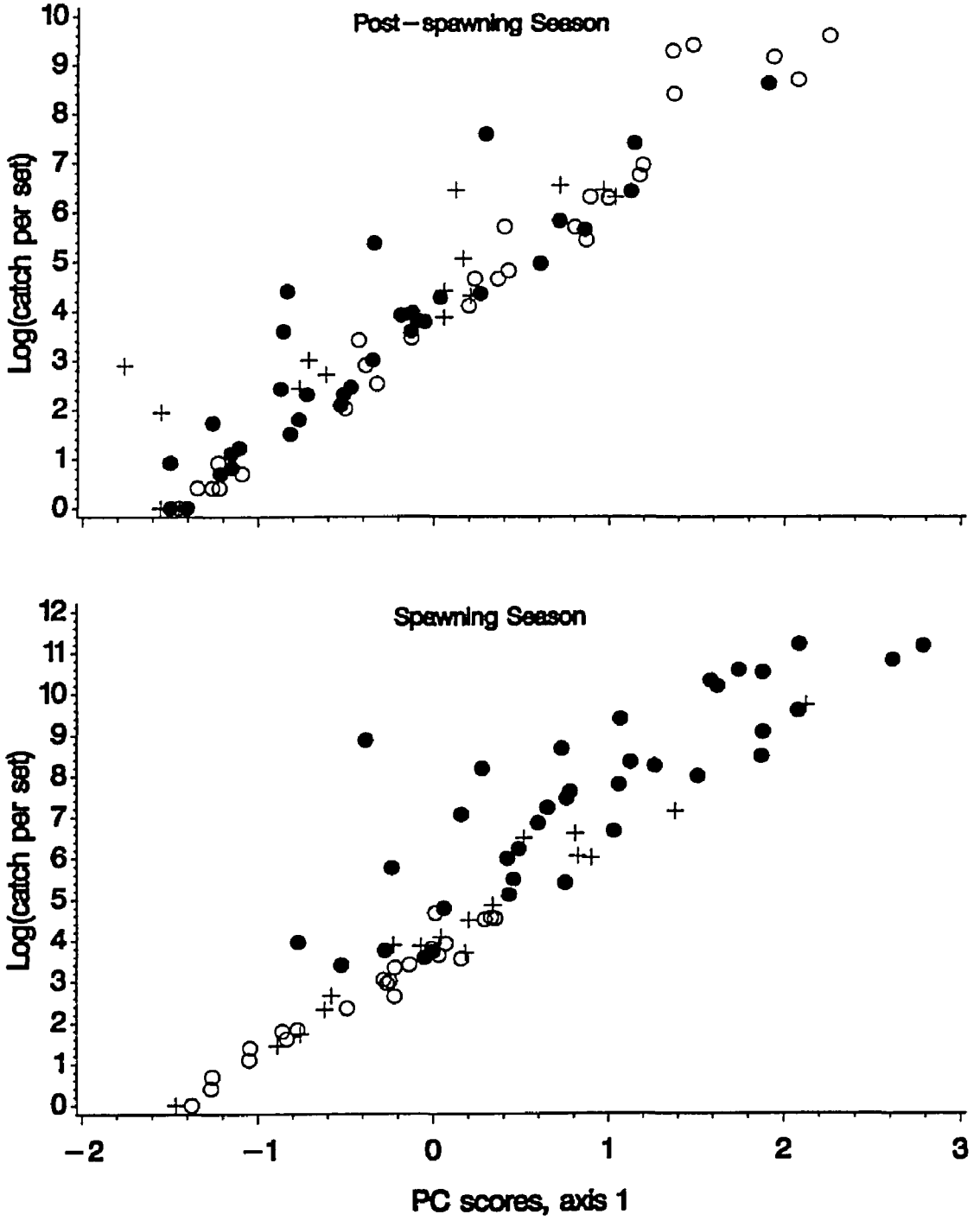

Figure 3.5. Relationship of the small seatrout abundance index to the first principal component scores (rotated PC factor, axis 1) for both the post-spawning (top graph) and spawning (bottom graph) seasons. Estuarine zones are shown as open circles (upper), pluses (intermediate), and closed circles (lower).

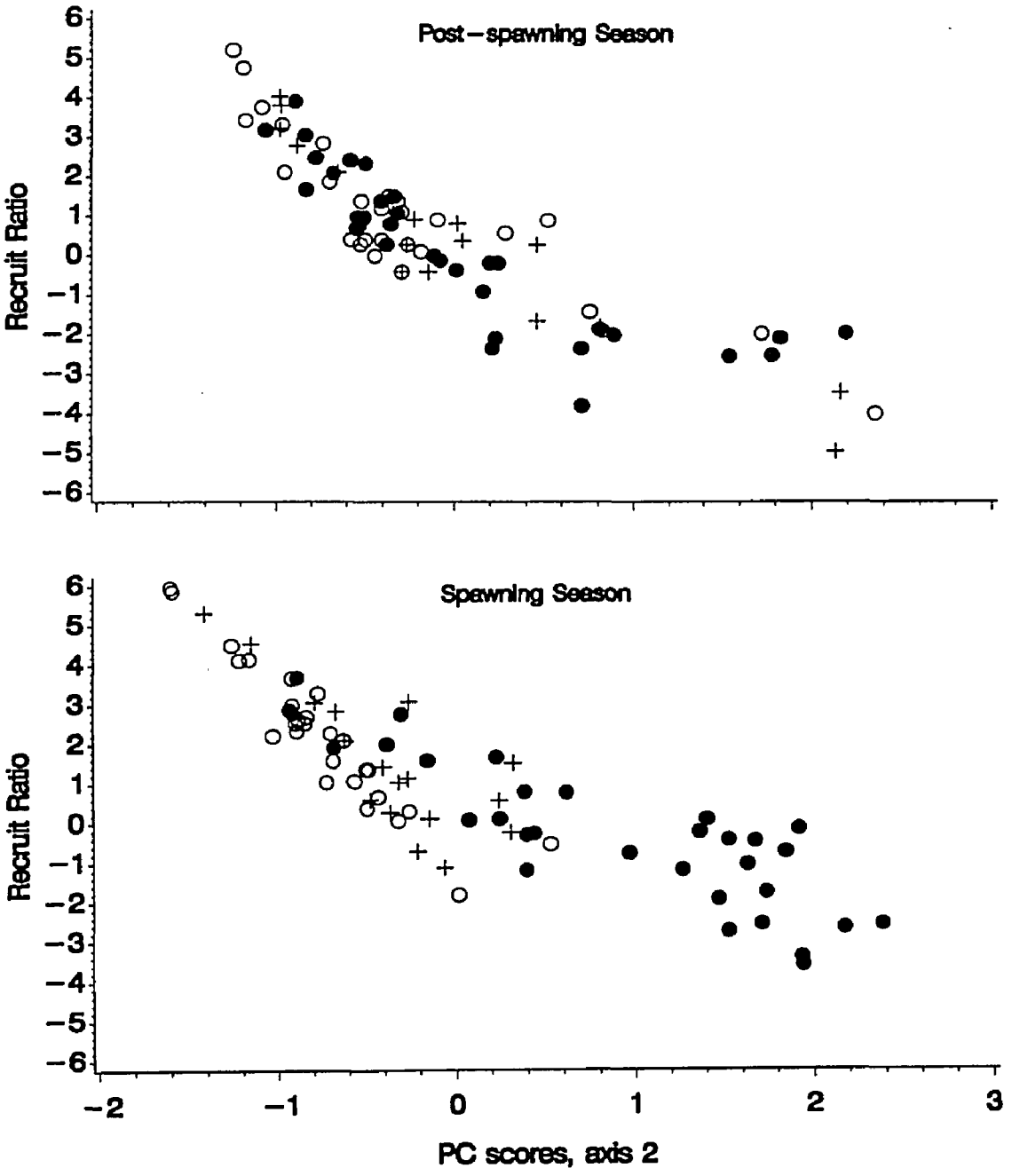

Figure 3.6. Relationship of the large seatrout abundance (measured as recruit ratio index) to the second principal components scores (rotated PC factor, axis 2) for both the post-spawning (top graph) and spawning (bottom graph) seasons. Estuarine zones are shown as open circles (upper), pluses (intermediate), and closed circles (lower).

(May-Aug.) seasons to further illustrate the distinct separation of the abundance (and size) information between the various estuarine zones identified by the cluster analysis.

For the purposes of the following statistical analyses we identify the first and second factors from the PCA as recruit and spawner abundance, respectively, and defer a biological rational for the interpretation of these factors to the discussion section of this paper.

General Linear Models

Results of the GLM analysis applied to each factor and directly to the CPUE data was highly significant in all cases ($p<.001$) and accounted for 52% and 51% of total variation in the data for the recruit and spawner models, respectively (Table 3.4). Many of the effects in the PC factor GLM appear to correspond fairly well to the factor interpretations of the GLM and the actual recruit and spawner seatrout catch data. The effects shown in table 3.4 represent only those which were significant in at least one of the GLM's out of a larger number of possible effects which included up to the highest order interaction between year, basin, season, and zone. The GLM included basin as a block to partition much of the variation which occurred in the both the recruit abundance (factor 1) and spawner abundance (factor 2) models. This effect suggests that seatrout abundance varies numerically between basin systems. This is not unexpected given the significant differences in marsh area and production (primarily and secondary) which occur in the different estuarine systems in coastal Louisiana (Deegan and Thompson 1985).

Table 3.4. Results of the General Linear Models analysis showing analysis of variance for the various spatiotemporal effects on the first two principal component factor scores and recruit and spawner Log_e(CPUE). F-value and probability of greater F are given for each model effect. Effects shown are those which were significant ($p<0.05$) in at least one of the models.

	GENERAL LINEAR MODELS							
	FACTOR 1		FACTOR 2		RECRUIT ABUNDANCE		SPAWNER ABUNDANCE	
EFFECT	F-value	Pr.>F	F-value	Pr.>F	F-value	Pr.>F	F-value	Pr.>F
MEAN SALINITY	10.23	0.001	0.03	N.S.	7.70	0.0006	3.69	N.S.
BASIN	8.24	0.0001	1.97	N.S.	10.44	0.0001	6.84	0.0002
YEAR	0.94	N.S.	8.86	0.0002	2.81	N.S.	10.61	0.0001
SEASON	13.71	0.0001	0.77	N.S.	15.22	0.0001	2.59	N.S.
ZONE	2.94	N.S.	3.35	0.037	5.22	0.006	8.13	0.0004
SEASON X YEAR	4.15	0.003	1.10	N.S.	3.57	0.008	1.79	N.S.
ZONE X YEAR	6.66	0.0001	1.13	N.S.	5.17	0.0006	0.97	N.S.
SEASON X ZONE	9.59	0.0001	5.45	0.0003	15.02	0.0001	14.87	0.0001
MODEL F-VALUE	5.47	0.0001	3.78	0.0001	6.41	0.0001	7.22	0.0001
MODEL R^2	0.453		0.364		0.522		0.509	

N.S. = NOT SIGNIFICANT AT $\alpha = 0.05$.

Spawning seatrout abundance (factor 2) also appears to vary significantly ($p<0.001$) over the three years of this study, but not significantly as an interaction effect over the spatiotemporal scales used in this analysis (table 3.4). Recruit abundance (factor 1) over years does, however, vary significantly with season and zone ($p<0.001$). The significant year, year x season, and year x zone interaction effects (season and zone) in the models probably arise due to an overall decrease in the gillnet catches of spotted seatrout from 1988 to 1990. Declines in the experimental gillnet catches of spotted seatrout (and probably abundance) in Louisiana between 1989 and 1990 were documented and suggested by Helser et al. (1991) to represent increases in natural mortality brought about by a severe freeze in the winter of 1989. Despite these highly significant model effects and their possible interpretation, the season x zone interaction appears most dominant and interesting.

The GLM analysis indicate that both recruit abundance (factor 1) and spawner abundance (factor 2) of the spotted seatrout population vary significantly ($p<0.001$) over the defined spatiotemporal scales of season and estuarine zone (Table 3.4). Indeed, the season x zone interaction in each of the models accounted for the greatest proportion of the total variation in the data (high F-values relative to the other effects). The lack of significance for the interaction between season x zone with year or basin indicates that the season-zone pattern remains constant over the years and within each basin system. The interactive effects of estuarine zone and season for each model are shown graphically in figures 3.7 and 3.8. Here, mean spawning seatrout abundance is

significantly greater in the lower estuarine zone (15-30 ppt) than both the upper and intermediate ($p<0.01$) zones during the spawning season (May-Aug.). Although mean spawning-size abundances do not differ significantly between any of the estuarine zones during the pre-spawning season (Jan.-Apr.) a pattern of increasing abundance from the upper to lower zone is similar for both these seasons (Figure 3.7). Catch rates for both male and female spotted seatrout taken without regard to size category (Figure 3.8) also show statistically greater abundances ($p<0.01$) in the lower estuarine zone than in either of the other zones.

The zonal distribution of recruit seatrout over the various seasonal scales also suggests a pattern similar to the spawners as abundance gradually increases from upper to lower estuarine zones during the spawning season (figure 3.7). Here, the upper (0-9 ppt) and intermediate (10-14 ppt) estuarine zones differs significantly from the lower (15-30 ppt) zone ($p<0.01$), although abundance of recruits in the upper zone remains comparatively higher than the spawners ($p<0.01$) in the same zone and over the same time period. Figure 3.8 further suggests that the relatively greater abundance of recruits in the upper zone during the spawning season is comprised primarily of female seatrout.

During the post-spawning season (September-December) the spawning size seatrout show no preference to estuarine zone, but disperse and become more or less uniformly distributed over all estuarine zones (Figure 3.7). However, recruit abundance after the spawning season is significantly greater ($p<0.01$) in the upper estuarine zone than the lower zone where their abundance was greatest only months before (Figure

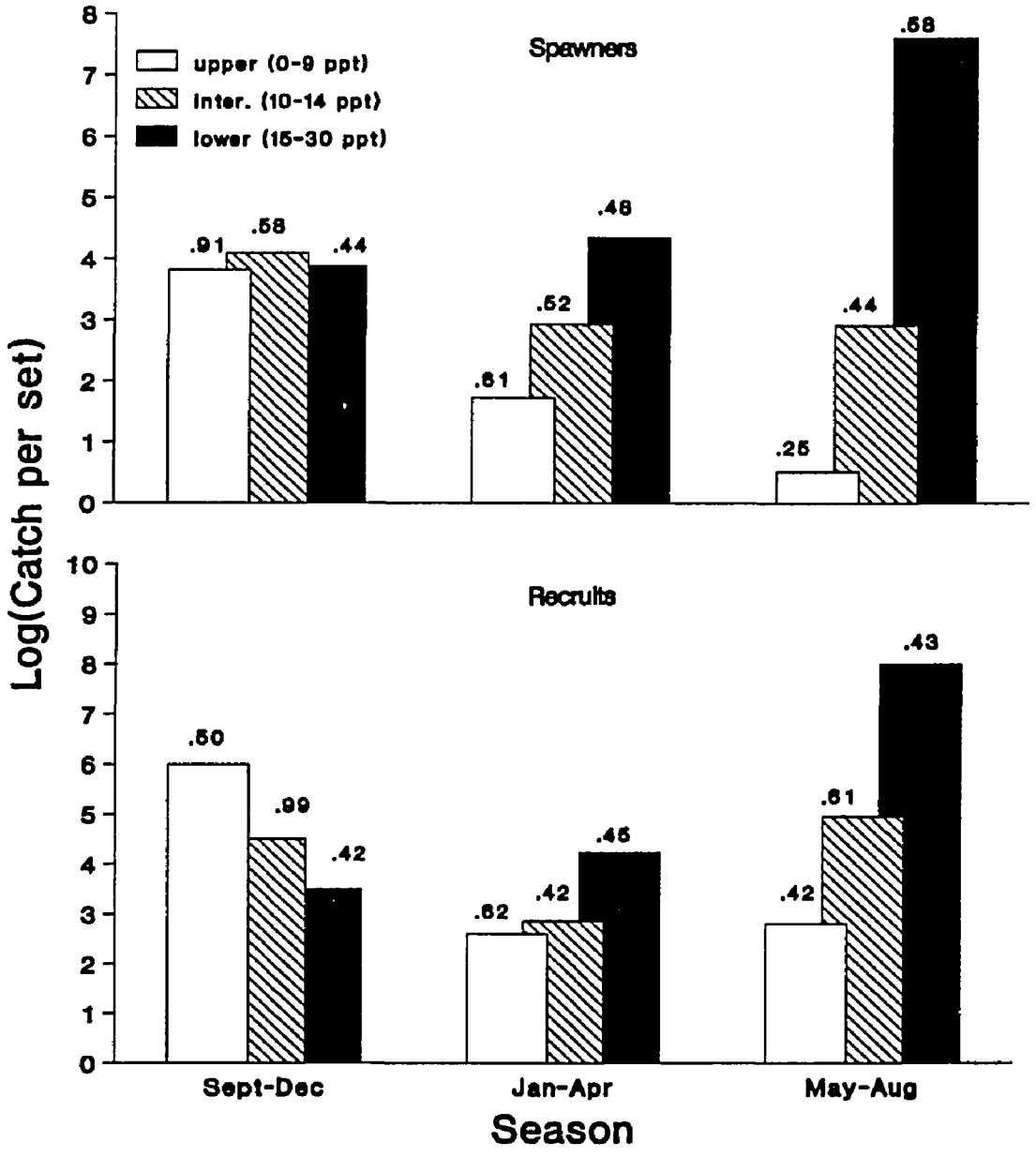

Figure 3.7. Comparison of spawner and recruit spotted seatrout abundance indices over the various seasons and estuarine zones. Standard errors are given above each bar histogram.

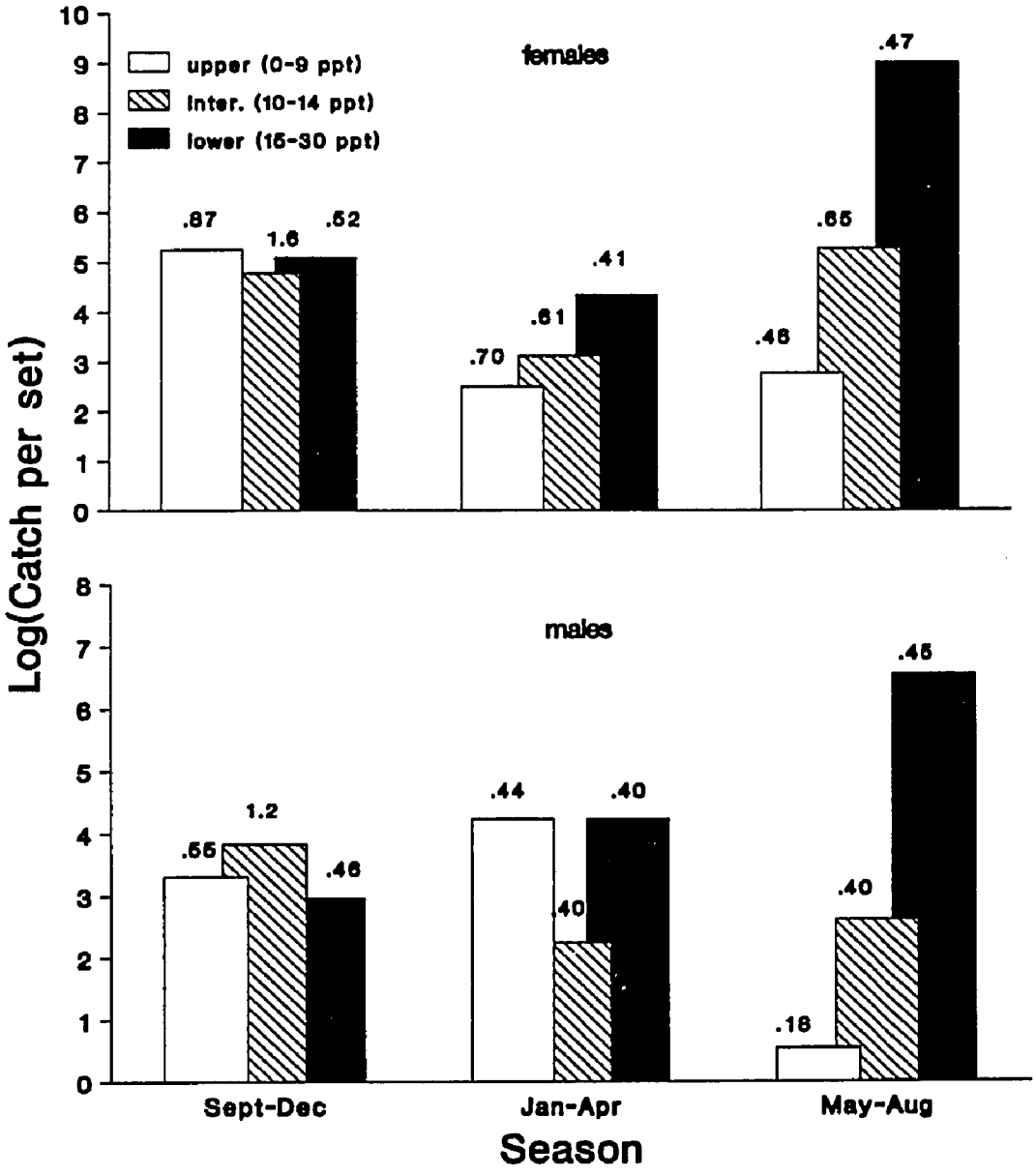

Figure 3.8. Comparison of overall male and female spotted seatrout abundance indices over the various seasons and estuarine zones. Standard errors are given above each bar histogram.

3.7). The GLM for the recruit size seatrout does indicate a highly significant ($p<0.001$) salinity component (Table 3.4) and suggests that recruit abundance is highly correlated with salinity.

Regression analysis of recruit seatrout abundance on salinity show that salinity interacts significantly ($p<0.01$) with season and that during the spawning season the relationship is positively correlated while negatively correlated during the post-spawning season (Figure 3.9). We also found a significant positive correlation between spawner abundance and mean salinity during the spawning season (Figure 3.9), although salinity did not appear as a significant effect in the GLM for spawner abundance (Table 3.4). The reason for this is probably due to the fact that spawner abundance is significantly correlated to salinity only during the spawning season. We tested whether regression slope coefficients varied between the estuarine systems using an analysis of covariance. No significant differences ($p<0.05$) were found in the abundance-salinity regression equations (recruit or spawner) between any of the four different estuarine systems over the spawning season. During the post-spawning season, the recruit abundance-salinity regression slopes also did not vary significantly ($p<0.05$) between any of the estuarine systems west of the Mississippi River, however, in the Breten Sound system recruit abundance was found not to be correlated to salinity. These results may indicate that the recruit abundance-salinity relationship can not be generalized over all estuarine systems in coastal Louisiana. Although an analysis of additional physical variables may be needed to more fully characterize this phenomena, it is possible that differential salinity regimes east

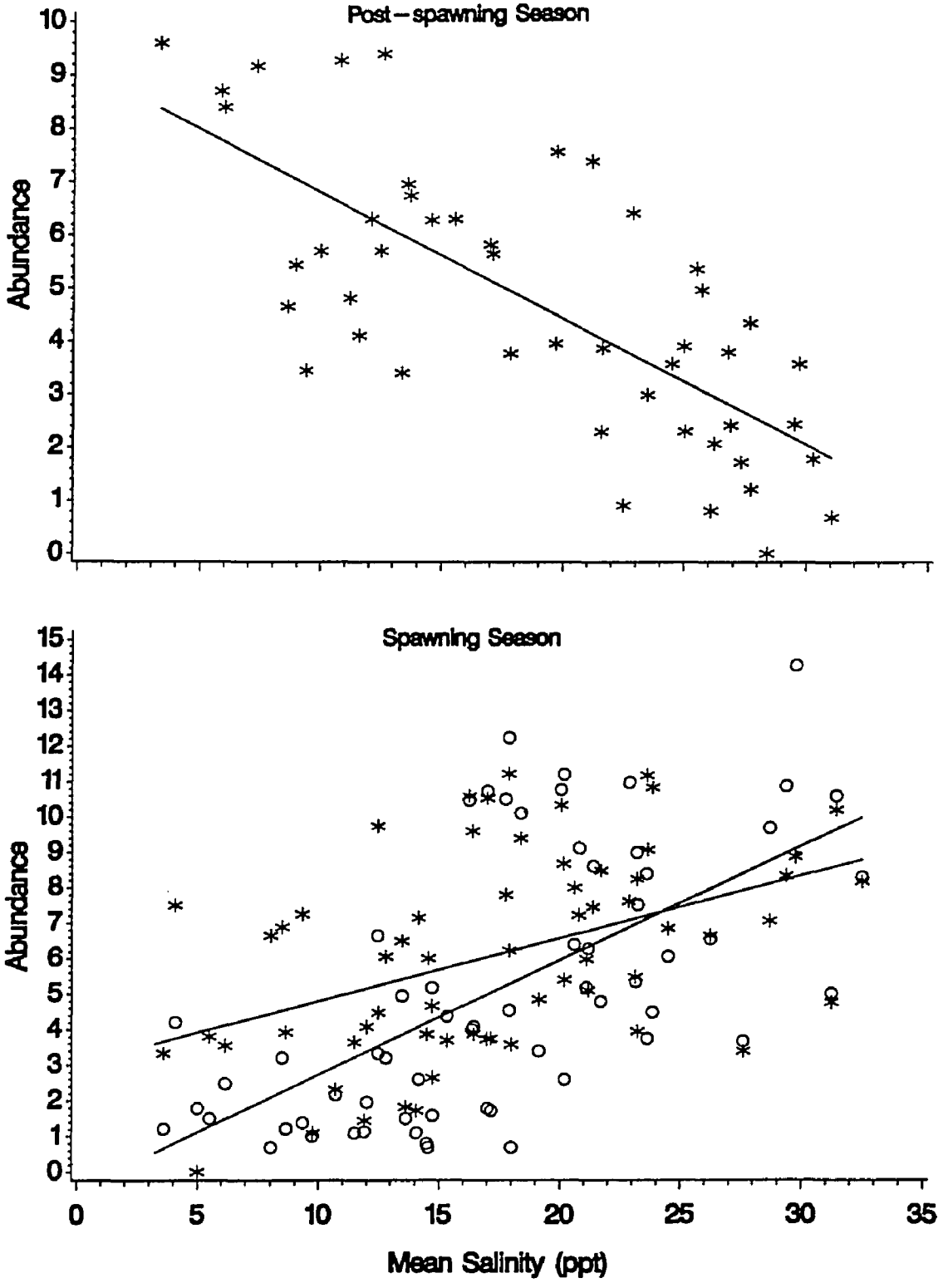

Figure 3.9. Regression equations and data scatter of recruit (stars) and spawner (open circles) abundance indices on mean salinity.

and west of the Mississippi River may in part be responsible. The spawning season regression lines for recruit abundance and spawner abundance (X) on salinity (Y) varied significantly ($p<0.05$). These regression equations are:

$$Y = 2.01+0.215*X \ (r^2 = 0.45), \text{ for recruit abundance, and}$$

$$Y = -1.04+0.346*X \ (r^2 = 0.51), \text{ for spawner abundance.}$$

The regression equation for recruit abundance on salinity during the post-spawning season is:

$$Y = 9.17-0.241*X \ (r^2 = 0.55).$$

Interestingly, the slopes for the recruit abundance-salinity relationships (which are highly significant, $p<0.001$), between the two differing seasons are nearly equal, but opposite, which suggests that the recruit abundance gradient with salinity is equal in magnitude between these two seasons.

Results thus far concerning the distributional ecology of spotted seatrout have been shown with regard to discrete segments of the population (i.e. recruit vs. spawning abundance) over both discrete and continuous spatiotemporal scales. It is also possible to examine spotted seatrout abundance on a continuous scale by estimating the population size compositions. We computed the seatrout population size compositions for the upper and lower estuarine zones over both the spawning and post-spawning season. Figures 3.10 and 3.11 show that the spotted seatrout population size composition varies substantially between the upper and lower estuarine zones over the spawning and post-spawning seasons. Although there appears to be considerable variation between years, the estimated population size structures suggests that

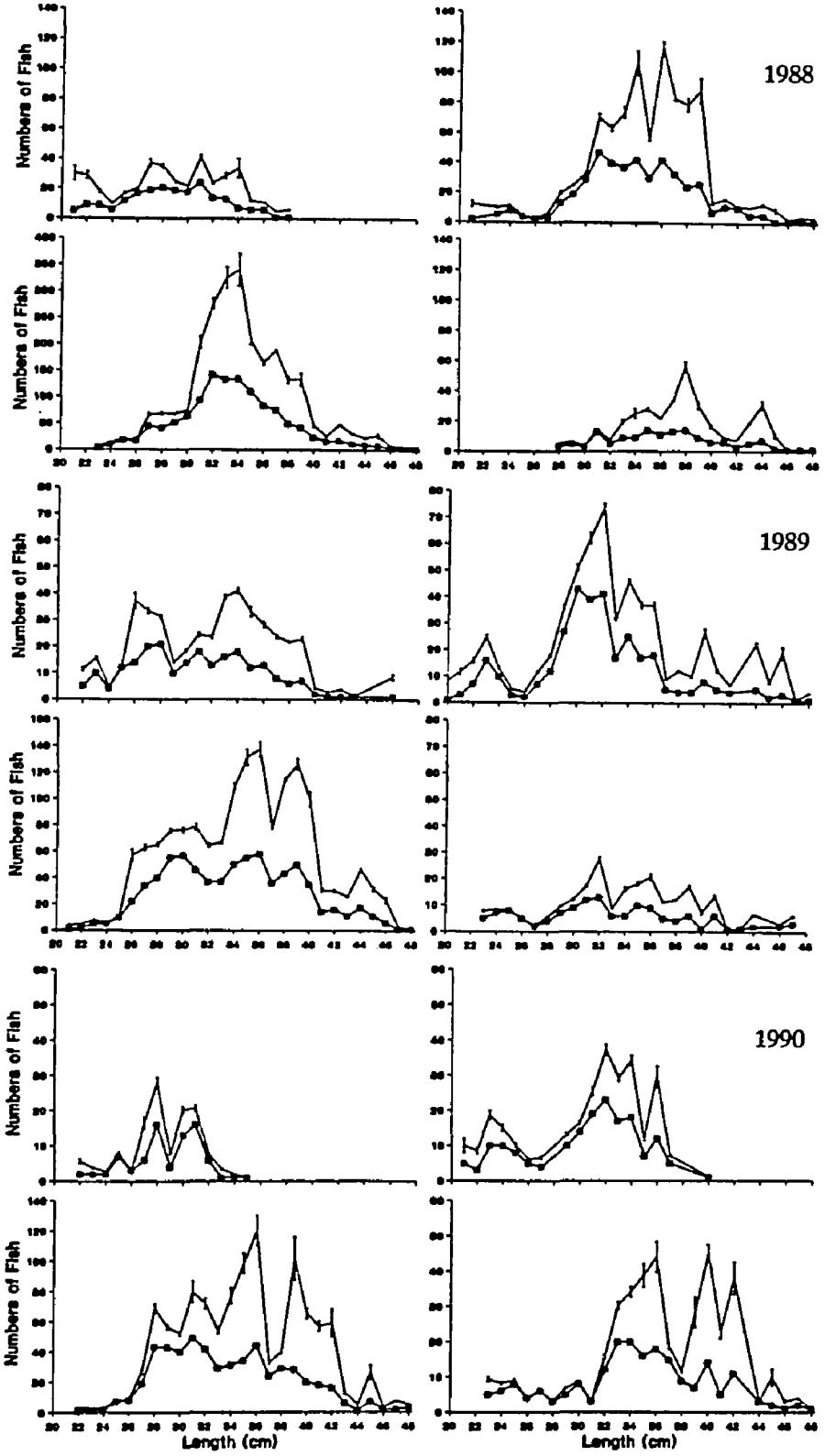

Figure 3.10. Estimated female spotted seatrout population size compositions during the spawning (left columns) and post-spawning (right columns) seasons in the upper (upper rows) and lower (bottom rows) estuarine zones for each year from 1988 to 1990. 95% confidence intervals around estimated relative abundances and observed gillnet catches (stars) by size-class are shown.

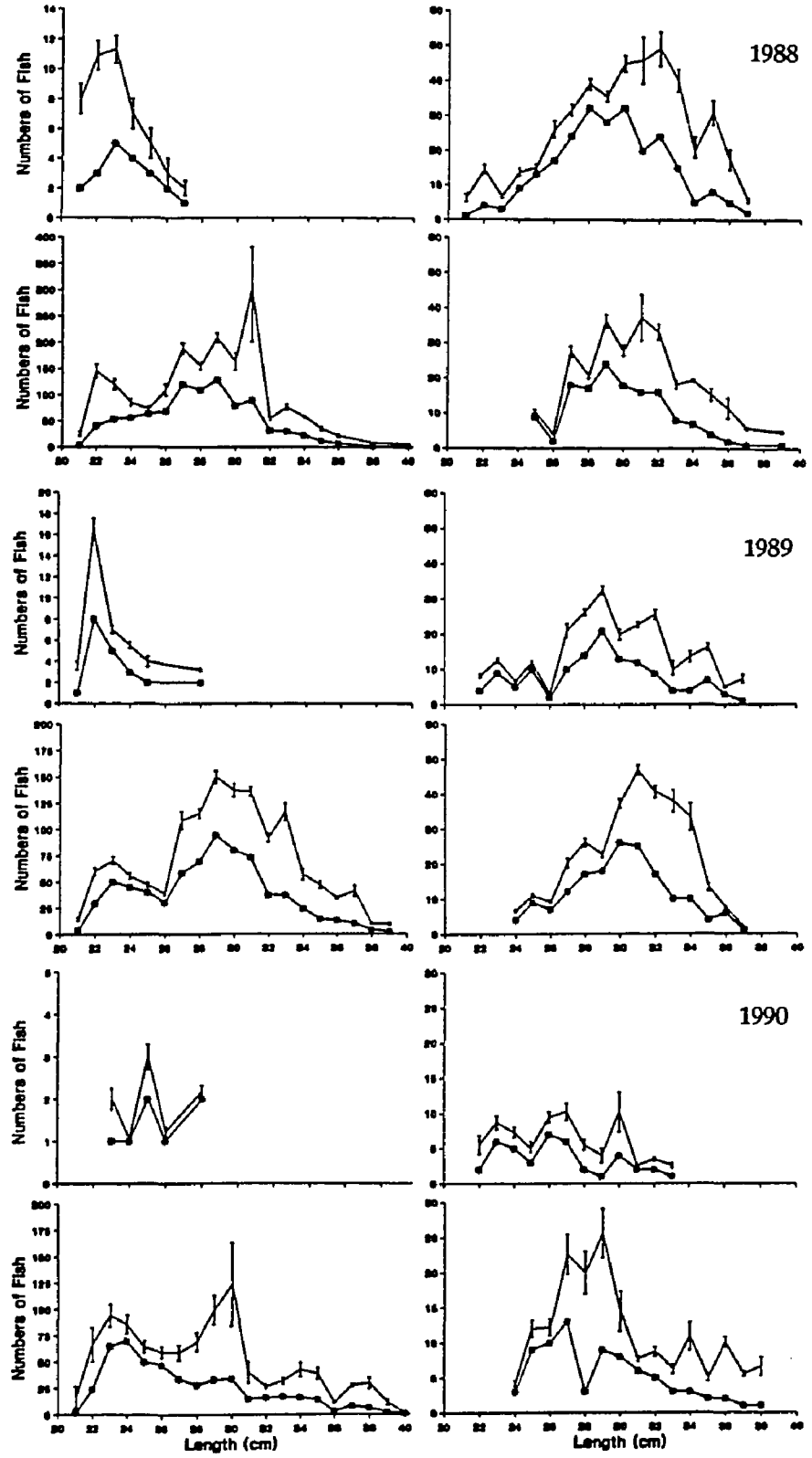

Figure 3.11. Estimated male spotted seatrout population size compositions during the spawning (left columns) and post-spawning (right columns) seasons in the upper (upper rows) and lower (bottom rows) estuarine zones for each year from 1988 to 1990. 95% confidence intervals around estimated relative abundances and observed gillnet catches (stars) by size-class are shown.

the greatest abundance of fish, male or female, occur in the lower estuarine zone during the spawn season, a result corroborated by the abundance-salinity relationships (for both recruit and spawner seatrout) shown in Figure 3.9.

Peak relative abundance of female and male seatrout in the lower zone occurs from 34 cm to 40 cm and from 28 cm to 32 cm, respectively (Figure 3.10 and 3.11). Most female and male seatrout in the upper zone during the spawning season appear smaller in size, where very few female seatrout greater than 34 cm are found in the upper estuarine zone during the spawning season (with the exception of 1989) and most males appear to have left the upper zone completely, although those which have remained are considerably small (approx. 23 cm).

Female size compositions during the post-spawning season indicate abundance is generally greater in the upper zone (Figure 3.10) and that the age structure is composed of both young (< age two) and older fish (up to age four). Numerous one year old female and male (23 cm) seatrout appear in the gear during the post-spawning and spawning season, respectively, perhaps suggesting that recruitment into the gear and/or fishing area increases gradually, beginning at about 23 cm (Figures 3.10 and 3.11). Males apparently become fully recruited at a smaller size (28 cm) than the females (32 cm) probably due to their maturing at an earlier age (or size) and participation in spawning activity.

Discussion

Spatiotemporal Scales

Clustering is a useful exploratory multivariate technique for searching data for a structure of "natural" groupings (Johnson and Wichern 1988). For the 28 stations distributed throughout 4 different basin systems it was logical to ask whether there were natural groupings based on the physical parameters which extend beyond the boundary of a single basin system. Station groupings from the clustering procedure (based on the various physical variables) support the notion that distinct physiochemical attributes can be associated with particular zones and that such zones may play an important role in governing the utilization of specific portions of the estuary by different life history stages.

In actuality, physical parameters, such as salinity, vary as longitudinal gradients in most Louisiana estuaries because of complex gravitational circulation patterns involving moderate inputs of fresh water and tidal influences (Day et al. 1989). However, estuarine ecologists attempt to define salinity gradients in terms of zones to facilitate the study of the organisms which are tolerant, and actually thrive, over a wide range of salinities. Most estuarine systems studied in Louisiana do exhibit a zonal salinity pattern and the definitions or saline limits to these zones have been characterized broadly as tidal fresh (0.0-0.5 ppt), mixing (0.5-25.0 ppt), and seawater (>25.0 ppt), although not all zones may be represented within a given estuarine system (Czapala et. al. 1991). The more well known (and specific) system of classification of salinity zonation applicable to estuaries in

Louisiana is the "Venice system" which subdivides the estuary into an Oligohaline (0.5-5 ppt), Mesohaline (5-18 ppt), and Polyhaline (18-30 ppt) zones (Bulger et al. 1990). Another more statistically based assessment was conducted using the actual distributions of organisms within certain salinity limits over the Mid-Atlantic region (Bulger et al. 1990) which found essentially five zones which overlap to some extent: fresh-4 ppt, 2-15 ppt, 11-19 ppt, 15-28 ppt 23-marine. Although a potentially useful classification, its application to Louisiana's estuaries is doubtful because of biogeographic differences and adaptational responses of organisms to environments with substantial sediment loaded fresh water input to the system.

The results of our statistical classification of the stations within the estuarine systems of Louisiana were more closely aligned to those of the Venice systems. However, the range of salinities of our upper zone classification is slightly broader than the oligohaline (0-5 ppt) while the intermediate zone is somewhat narrower than that given to the mesohaline (5-18 ppt) for the Venice system. These observations of the general salinity ranges (and classes) for each of the given estuarine systems in Louisiana are consistent with other reports (Czapla et al. 1991), particularly with regard to specific estuarine systems and the presence or absence of fresh water input.

Principal Components Analysis

The first two factors identified by the PC factor analysis were sufficient to separate the experimental gillnet catch data between the upper (low salinity) and lower (high salinity) estuarine zones,

particularly during the spawning season. This effect reinforces our notion that seatrout abundance and the non-arbitrary station groupings are statistically associated and that these associations are seasonally dependent (figures 3.4 through 3.6). Although most of the variation in the experimental gillnet catch data lie along the first PC factor axis, both PC factors are required to fully characterize the distribution of spotted seatrout abundance both in time and space.

It may be possible to associated a biological interpretation, other than simply a size discrimination, with the first two factors identified by the PCA factor analysis. We computed the percent of the fish caught by sex and mesh which exhibited a gonadal condition index of three or greater and identified these as mature, while those less than three were regarded as immature. The percentage of immature female spotted seatrout for the 2.0, 2.5, 3.0, and 3.5 inch meshes were 43%, 34%, 24%, and 23%, respectively. Although a greater fraction of the total numbers of male fish caught by each mesh were mature compared to females, the 2.0 inch mesh showed the largest percentage immature fish with 20% than any of the others (all others < 10%). These results suggest that the 2.0 and 2.5 inch meshes for the females and the 2.0 inch mesh for the males comprise a relatively larger fraction of immature seatrout than the other meshes within a given sex.

Additionally, the size at which male and female seatrout recruit into the gear and/or fishing grounds is approximately 27 cm and 32 cm, respectively (Helser et al. 1991). These sizes correspond to the expected size of fish captured by the 2.5 and 2.0 inch mesh for female and male seatrout, respectively. Thus, it may be reasonable to

interpret the first two PCA factors from a biological stand point. The first factor represents that segment of the seatrout population which has not yet fully matured and at the same time are not fully recruited into the fishable population. The second factor represents the mature fraction of the population which have become fully recruited.

Although the PCA technique gained fairly widespread use for the reduction and analysis a large number of species into smaller assemblages which presumably have some ecological relationship (Digby and Kempton, 1987), its application on the population ecology level appear equally as promising. Here we demonstrate its use for grouping certain size categories, as determined by an experimental gillnet, of a single species. We feel the results from the application of the PCA technique to the seatrout catch data from experimental gillnets (within the scope of this analysis) was indeed fruitful, particularly because of its interpretability and biological rational.

Distributional Ecology

The data presented in this paper strongly indicate that spotted seatrout abundance is statistically associated with a given estuarine zone depending on season and that differential distribution patterns are exhibited by individuals from different life history stages in the population (table 3.4, Figures 3.7 and 3.8).

Seasonally, higher catch rates have been reported during the spring and summer months in Louisiana by others (Juneau 1975; Adkins et al. 1979), although these authors do not indicate whether greater abundance during the spawning season is associated with a particular

spatial scale within the estuary. Czapla et al. (1991) show differences in temporal abundance of adult spotted seatrout in two out of the six systems they studied which are comparable to those studied here. Adult spotted seatrout in the Terrebone Bay system were more numerous during the summer months (May-July) while generally highest abundances in the Breton Sound system was from march through August. These authors also indicate that adult abundance of spotted seatrout in the Terrebone Bay system is greater in the marine salinity zone (>25.0 ppt) than either the tidal fresh (0.0-0.5 ppt) or mixing zones (0.5-25 ppt). Although valuable information, these authors did not integrate the spatial and temporal aspects of seatrout abundance with a statistical based analysis which would more fully characterize the distributional ecology of the species.

The spatiotemporal pattern of adult (spawner) abundance documented here may reflect the onset of spawning aggregations of spotted seatrout beginning in the early spring and becoming clearly evident during the summer in the higher salinity areas of the lower Bays and beaches of coastal Louisiana (figures 3.7 and 3.8). Spotted seatrout spawning aggregations during the summer months have been observed to be greater in higher saline waters, particularly near barrier islands and between passes (Saucier, 1991). Saucier (1991) found that spawning aggregations of spotted seatrout (as identified by hydrophone recordings) were significantly correlated to an interaction of salinity and current velocity. These physical conditions perhaps represent environmental

optima where spawning individuals congregate in the higher saline waters with greater current velocity to facilitate the survival and dispersal of fertilized eggs.

Our results suggests that a large segment of the adult spotted seatrout population respond behaviorally to some sort of predictable environmental cue to make a seasonal spawning related migration to the lower coastal zone during the appropriate time of year. Unexpected, however, was the large number of recruits which apparently responded in a similar manner. It is possible that many of the immature recruits, which have not yet reached the critical size, accompany the adults or spawners due to their intense schooling behavior. Some authors have suggested that temperature and photoperiod are the principal environmental factors (Cues) responsible for cyclical gonadal development in seatrout (Hein and Shepard 1983; Overstreet 1983; Brown-Peterson et al.1988; Saucier 1991) which probably pattern aggregational and migratory behavior .

The spatiotemporal distribution pattern of recruit (sub-adult) spotted seatrout during the post-spawning season indicated here is also corroborated by Czapla et al. (1991) who found greater juvenile abundance in the Mixing zone (0.5-25 ppt) during the early fall (Sept.-Nov.) in the Terrebone Bay system. These result suggests that recruits may preferentially seek the upper estuarine zone after the spawning season (Sept-Dec.). Moreover, our results are consistent with tagging studies in the Calcasieu Lake estuary in Louisiana which indicate a Gulfward movement of tagged seatrout in the early summer in conjunction with spawning and a subsequent return in the winter (Arnoldi 1984).

Arnoldi (1984) also indicates that a major segment of the population remained near the Gulf of Mexico for extended periods. Although this author did not differentiate between the size/age related movements, it might be hypothesized that the pre-recruit or juveniles make a return migration northward while adult abundance is fairly evenly dispersed as indicated by these data.

It is quite clear from fish community ecology studies that species tend to distribute themselves along salinity (and other environmental) gradients in response to their individual physiochemical tolerances and preferences (Weinstein 1980, 1985). The results from this study strongly suggest that abundance of both recruit and spawner spotted seatrout is correlated with salinity and that the strength and direction of the correlation is related to the life history stage (figure 3.9). Other studies have described significant correlations between abundance of estuarine fish assemblages and salinity (Deegan and Thompson 1985; Ross and Epperly 1985). Deegan and Thompson (1985) reported a significant positive correlation (r^2=0.66) of the abundance of marine finfishes (as a community of all marine forms) with salinity during the summer in several estuaries in Louisiana. The results of Ross and Epperly (1985) showed no correlation between salinity and *Cynoscion* spp in North Carolina estuaries, although many other of the estuarine-marine species of fishes which were studied exhibited a positive quadratic rather than a linear relationship. Other authors working with estuarine communities suggest correlations of abundance with environmental gradients are non-linear (Green 1971; Green and Vascotto 1978; Westman 1980). An interesting result from our work not shown by these others is

that juvenile spotted seatrout abundance (a marine-estuarine species) which exhibit a wide range of salinity tolerances (Tabb 1959, Mahood 1979; Czapla et. al 1991; Saucier 1991) show both a positive and negative correlation with salinity depending on the season (figure 3.9).

Although it might be compelling to conclude that the observed relationships with salinity (whether linear or quadratic) represent preferred values that individuals actively seek, the possibility of other factors (biotic or abiotic) associated with salinity can not be ruled out. For instance, it seems likely that, during the spawning season, the spotted seatrout population as a whole (recruit and spawner seatrout abundance) is oriented toward the higher salinity waters of the lower bays and beaches of coastal Louisiana estuaries in response to favorable environmental optima for spawning. Simultaneously, these individuals may be taking advantage of greater resource available in the lower coastal zone during this time. Further, the reverse gradient of sub-adult seatrout with salinity during the post-spawning season (figure 3.9) may be an upestuary movement which coincides with an inshore migration by juvenile marine species such as Bay anchovy and menhaden (Deegan and Thompson 1985). This could provide not only a prey species for the sub-adult seatrout to exploit but also a refuge from predation afforded by greater vegetative covering in the upper reaches of the estuary.

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CHAPTER IV

A Monte Carlo-Based Virtual Population Simulation for Incorporating Uncertainty into Estimates of Spawning Potential Ratios, an Application to the Spotted Seatrout Fishery in Louisiana

Introduction

Many fish stock assessment models which serve as the basis for management decisions are deterministic, that is a given set of input parameter estimates results in a unique output solution. The virtual population assessment (VPA) model originally developed by Fry (1949) and applied by Gulland (1965) and Murphy (1965) is by nature deterministic and statistically overparameterized. The basic VPA model has been adapted to more sophisticated approaches, some of which utilize abundance (e.g. catch per unit effort) indices to "tune" the analysis (Deriso et al. 1984, Pope and Shepard 1985, Vaughan et al. 1988). Other studies have examined the sensitivities in input parameter uncertainty (Jones 1984, Hilden 1988, Sampson 1988) and variances (Deriso et al. 1985, Prager and MacCall 1987, Gavaris and Gavaris 1988), which have generally focused on uncertainty associated with VPA estimates of population size and fishing mortality rates. Lewy (1988) developed an integrated stochastic VPA to estimate precision of other stock descriptors, such as spawning stock biomass. His model is fairly complex, utilizing catch and effort data, abundance indices, and a maximum likelihood estimation procedure. However, when auxiliary

information on the stock is unavailable (adequate catch and effort data, CPUE indices) to supplement the VPA another method must be utilized to characterize the uncertainty in the model output.

Much of the information required for a more sophisticated approach to the assessment of the spotted seatrout stocks in Louisiana are lacking, and the data which are available, in particular mortality rates, represent point estimates without associated estimates of variation. Without appropriate techniques to characterize the uncertainty associated with assessment model output management can not provide adequate advice relevant to the risks involved in setting incorrect biological reference points, such as SSBR levels.

This study attempts to quantify the uncertainty associated with the stock assessment approach and the biological references points currently being used by the state to manage the spotted seatrout stocks. Presented here is a Monte Carlo-based simulation method applied to simple (i.e. overparameterized) virtual population analysis to investigate the affect of input parameter uncertainty on the precision of model output. We first quantify the direction and magnitude of the potential biases associated with wrong choices in input parameter selection and then assess the affect of input parameter uncertainty on the precision of estimates of spawning potential ratios (SSBR; Gabriel et al. 1989) and recruitment to age 2. The application of this simulation technique is illustrated first on a hypothetical catch-at-age vector generated with available information from the fishery for spotted seatrout and then applied to the actual catch data from the spotted seatrout fishery.

Methods

VPA Model

The computational approach used here to estimate the population size and the fishing mortality rates were based on the iterative solution described by Schumacher (1970) and found in Jones (1984). This approach was adopted by the fishery managers in the state and serves as the basis for the management of the seatrout stocks. Here, each VPA run consisted of a selection of natural mortality (M, assumed constant across ages) and a terminal fishing mortality (F_t, input for the terminal age in the fishery), either randomly from the specified input distribution (for the Monte Carlo simulations) or deterministically (for seatrout catch-at-age simulation). At each age (t) for the catch-at-age vector (simulated or otherwise) the objective function

$$f(F_i) = \exp(-Z_i)/U_i - Q_i \qquad (4.1)$$

where: i = iteration step, i.e. $F_i = 0.001$

F_i = the instantaneous fishing mortality

Z_i = the total instantaneous mortality

$U_i = F_t*(1-e^{-Zt})/Z_t$, the exploitation rate.

$Q_i = V_{t+1}/C_t*E_{t+1}$, which is the constant in the integration of Baronov's catch equation.

C_t = Catch of fish at time *t*.

V_t = The "virtual population" at time *t*, or the number of fish "destined" to be caught over the remainder of the life of the year-class.

E_t = The proportion of fish alive at the beginning of time *t* that are subsequently captured.

was solved iteratively for a value of F_i. For example, starting with a value of 0, F_i was incremented by 0.001 such that the quantity on the right hand side of the equation converged sufficiently close to 0. This iterative process was continued backwards at each age, and estimates of population size and fishing mortality rate at age (F-vector) were obtained. The solutions obtained from the VPA were used to generate estimates of spawning stock biomass per recruit (SSBR) described by Gabriel et al. (1989). Using the estimated population size at age 0 (N_0) and the F-vector (F_t) derived from the VPA, as well as constant M at each age, the surviving numbers at age were computed by, $N_t = N_0 * e(-F_t+M)$, and multiplied by the average weight at age (Weiting 1989) to estimate female biomass at age. For these computations we assume a knife-edge maturity schedule, beginning at age 2 for lack of sufficient maturity at age data. The sex ratios were assumed to be 1:1 and constant across ages. Total female spawning biomass was computed as the sum over all age groups beginning with age 2. Finally, SSBR was estimated as the ratio of the total female spawning biomass to that which would have existed without removals due to fishing (i.e. when F=0).

Catch-at-age (Cohort) Simulation

To simulate a cohort of spotted seatrout, we used a set of fixed control parameters to derive a hypothetically known catch at age vector. The control parameters we used (estimated F-vectors and population sizes at age zero) were generated from VPA runs conducted on the

Louisiana spotted seatrout catch data from 1980 through 1990, estimated by the Louisiana Department of Wildlife and Fisheries (LDWF 1991).

Several adjustments were made to the cohort data prior to the analysis by the VPA. First, the terminal age for each cohort was set to age five and greater since the age and growth study used to convert lengths to ages was based on a maximum observed age of five years old (Weiting 1989). Secondly, the VPA analysis was conducted only on the 1980 to 1986 cohort since the 1987 and younger cohorts of fish were not in the fishery long enough to produce an observed catch greater than age 5. The later years (greater than 1987) were excluded to minimize errors which may result from catch projections, and particularly since numerous regulation changes in 1987 would result in altered fishing patterns after that year. Table 4.1 provides the spotted seatrout catch data, arranged by cohorts from 1980 through 1986, upon which the initial VPA runs were conducted to generate the control parameters with which we simulated a catch-at-age vector.

For this VPA analysis we set the annual natural and terminal fishing mortality rates at 0.3 and 0.4, respectively. Evidence from unpublished studies and the published literature for spotted seatrout (*Cynoscion nebulosus*) suggested a value close to 0.3 for M (Beverton and Holt 1959, Samane and Okado 1973, Condrey et al. 1985, Weiting 1989), although estimates ranged from 0.114 (Wakeman and Ramsey 1985) to 0.456 (Rutherford 1982). Reported estimates of instantaneous fishing mortality for spotted seatrout in the Gulf of Mexico ranged from 0.32 to 1.44 (Klima and Tabb 1959, Stewart 1961, Iversen and Moffet 1962, Rutherford 1982, Colura et al. 1984). However, there is little directed

Table 4.1. Catch at age data for the 1980 through 1986 cohorts of spotted seatrout in Louisiana.

Age (years)	Cohort 1980	1981	1982	1983	1984	1985	1986
0	27,082	1,508	81,870	15,218	11,112	40,065	3,174
1	1,580,939	2,511,402	3,222,204	582,995	2,748,310	7,249,248	4,270,316
2	2,295,775	2,740,414	946,354	2,002,249	3,534,904	3,808,288	3,421,995
3	501,789	296,764	526,164	789,882	429,534	737,799	511,147
4	55,442	73,138	179,309	109,009	202,247	134,411	251,302
5>	53,038	73,138	171,535	104,283	193,479	137,194	240,408

harvest of age 4 and greater spotted seatrout in Louisiana (LDWF 1991). Therefore, it is likely that the estimates reported above may be too high. Based on this information we somewhat arbitrarily set F_t to 0.4.

The annual natural and age-specific (estimated from the VPA) fishing mortality rates were divided by 365 to derive daily fishing mortality rates which were then weighted by the daily proportion of the total annual Louisiana spotted seatrout catch based on Marine Recreation Fishing Statistics Surveys (MRFSS). The daily catch was then computed based on Baronov's (1932) catch equation:

$$C_i = N_i * F_i * [1-\exp(-(M_i+F_i))]/(M_i+F_i) \qquad (4.2)$$

Where: i = daily interval

C_i = Catch of fish in the ith interval

N_i = Surviving number of fish at the beginning of the ith interval (e.g. $N_i=N_0*\exp(-(M_i+F_i))$.

F_i = Instantaneous rate of fishing mortality

M_i = Instantaneous rate of natural mortality

The simulated catch at age vector was taken as the sum of the catches over the daily intervals for each age group. To assess the potential biases associated with a wrong choice in the input parameters we ran the VPA on the simulated cohort using three different levels of natural mortality; 0.2, 0.3, and 0.4. Within each level of natural mortality, the terminal fishing mortality rate was set at 0.2, 0.4, 0.7, and 0.9.

Monte Carlo Simulation

The Monte Carlo simulations used in this study involve the recomputation of SSBR and recruitment to age 2, where each VPA run is

parameterized by a value of natural mortality (M) and terminal fishing mortality (F_t) each randomly selected from a specified input distribution. The choice of probability distribution for a given input parameter should represent the uncertainty associated with that parameter. Since natural mortality and terminal fishing mortality are difficult estimates to obtain parametrically, they are more often regarded as "best guesses" using some biological intuition on the part of the biologist and their specified input distributions must be characterized by another means. Pauly (1980) and Hoenig (1983) have utilized more analytical methods to derive estimates of natural mortality and their associated precision.

We examined two possibilities of describing uncertainty in the input parameters for the Monte Carlo simulation; the uniform and triangular probability distributions. These we felt best represented the random nature of input parameters given the lack of estimate precision reported in the literature. For the uniform input distribution, all parameter values within a specified range have an equal probability of being selected as the true one. This distribution may serve best when one has no a priori basis of selecting one value over another. When one has an a priori knowledge of the most likely parameter value as being the true one, the triangular input distribution may be a more logical choice. Here the mode, representing the most likely value, can fall anywhere within a specified range. This may be the case when the literature for a given species contains a number of coincidental values for a particular estimate within some range.

For the method presented here, we chose to examine the model output using input parameters randomly selected from both the uniform and triangular input probability distributions. The range of natural mortality used for both the uniform and triangular probability distributions was set at 0.114 to 0.486 based on available estimates in the literature (Wakeman and Ramsey 1985, Rutherford 1982). The modal (most probable) value used for the triangular input distribution was set at 0.3. The range for terminal fishing mortality used in both the uniform and triangular input distributions was set at 0.10 to 0.70 with the mode for the triangular distribution set at 0.40. The range for F_t used for the Monte Carlo simulations was shifted downward as compared to the reported literature (0.32 to 1.44) to account for decreased fishing on age four and older fish. A total of 3000 VPA simulations were conducted using a fortran 77 program on a model 3084 IBM mainframe computer.

Results and Discussion

The estimated age-specific fishing mortality rates and population sizes at age from the initial VPA runs on the 1980 to 1986 cohorts of spotted seatrout are given in tables 4.2 and 4.3, respectively. Estimated F-vectors run only to age 4 and greater as these initial VPA runs were parameterized at the terminal age 5 with F_t=0.4. The seven year average fishing mortality vector from age 0 to 4 (terminal F=0.4 at age 5 initiated the VPA) indicated in table 4.2 and the average population size at age 0 (Table 4.3), were used as the control

Table 4.2. Virtual Population Anaylsis estimated age-specific instantaneous fishing mortality rates for the 1980 through 1986 seatrout cohorts. Natural mortality (0.3) and terminal fishing mortality (0.4) indicated were used as input parameters for each cohort.

Age (Yrs)	Cohort 1980	1981	1982	1983	1984	1985	1986	Avg. Fishing Mortality
0	0.0350	0.0010	0.0091	0.0021	0.0010	0.0021	0.0010	0.0028
1	0.3113	0.4295	0.6442	0.1136	0.3337	0.6776	0.4589	0.4241
2	1.2031	1.4741	0.4467	0.7951	1.1233	1.1389	0.9731	1.0220
3	1.1679	0.6953	0.5476	1.0176	0.4247	0.8197	0.4101	0.7261
4>	0.4098	0.4101	0.4101	0.4101	0.4101	0.4101	0.4101	0.4100

Table 4.3. Virtual Population Analysis estimated population size at age for the 1980 through 1986 seatrout cohorts. Natural mortality (0.3) and terminal fishing mortality (0.4) were used as input parameters for each cohort.

Age (Yrs)	Cohort 1980	1981	1982	1983	1984	1985	1986	Avg. Population. Size
0	9,194,990	11,115,176	10,528,616	8,476,996	15,020,224	22,676,408	17,919,946	13,561,765
1	6,577,527	8,226,095	7,729,134	6,226,739	11,116,134	16,763,855	13,262,154	9,991,663
2	3,569,262	3,966,212	3,006,561	4,143,978	5,898,497	6,306,779	6,209,090	4,728,625
3	793,945	672,812	1,166,604	1,109,663	1,421,052	1,495,896	1,738,312	1,199,755
4	182,932	248,680	499,822	462,530	688,457	488,227	854,545	489,313
5	89,955	122,250	245,710	227,337	338,442	240,010	420,090	240,548

Table 4.4. Computation of female spawning stock biomass under conditions of fishing (F>0) and no fishing (F=0) for the simulated cohort of spotted seatrout. Catches shown are those for the simulated cohort generated from control parameters. Spawning stock biomass per recruit (SSBR) is computed as the ratio biomass F>0/F=0.

Age (Years)	Catch	Avg. Length (mm)	Avg. Weight (kg)	F > 0		F = 0	
				Numbers	Biomass (kg)	Numbers	Biomass (kg)
0	30,474	-	-	13,561,765		13,561,765	
1	2,848,715	219.6	0.105	9,230,663	973,357	9,256,237	976,117
2	2,593,985	362.9	0.468	4,421,839	2,072,547	6,857,189	3,214,012
3	396,261	452.9	0.905	1,109,283	1,003,947	5,079,931	4,597,548
4	149,932	509.5	1.283	519,507	666,781	3,763,305	4,830,153
5	74,366	545.0	1.567	257,588	403,682	2,787,925	4,371,073
6	36,888	567.3	1.766	127,672	225,499	2,065,346	3,647,907
7	18,298	581.3	1.898	63,280	120,167	1,530,046	2,905,543
8	9,076	590.1	1.985	31,364	62,278	1,133,486	2,250,722
9>	8,867	595.6	2.041	15,545	31,734	839,707	1,714,200
						SSBR = 0.165	

parameters to simulate the hypothetical catch-at-age vector for the spotted seatrout cohort. For the simulation, Age 9 was set as the terminal fishing age based on the concept that less than 5% of the cohort lives beyond age 3/M in an unfished condition; (Anthony 1982). Therefore, annual fishing mortality to age 9 was assumed constant beyond age 4 at 0.410 (Table 2). The simulated hypothetical catch-at-age vector from age 0 through 9 is given in table 4.4. This simulated cohort essentially represents the catch of spotted seatrout in Louisiana under equilibrium conditions during the earlier part of the 1980's. Also shown in table 4.4 is the computation of female spawning stock at age and spawning stock biomass per recruit (SSBR). The values given are the deterministic estimates for the control parameters used for this simulated cohort (Tables 4.2 and 4.3).

We examined the potential bias associated with a wrong choice of input parameter estimates using the simulated cohort which was generated from a set of assumed known control parameters. The biases in the model output are investigated in terms of the estimated population size and fishing mortality at age in figures 4.1 and 4.2, respectively. Figure 4.1 shows the percent error propagated in the VPA output conducted on the simulated cohort from a wrong choice in natural mortality and terminal fishing mortality. Here, choosing M = 0.2 results in under-estimating (negative bias) the population size at age for almost all of the ages in the simulated cohort while over-estimating M leads to over-estimates (positive bias) in population size. Note that the percent error in a wrong choice in natural mortality is compounded by a wrong choice in terminal fishing mortality, particularly when M=0.4 is chosen.

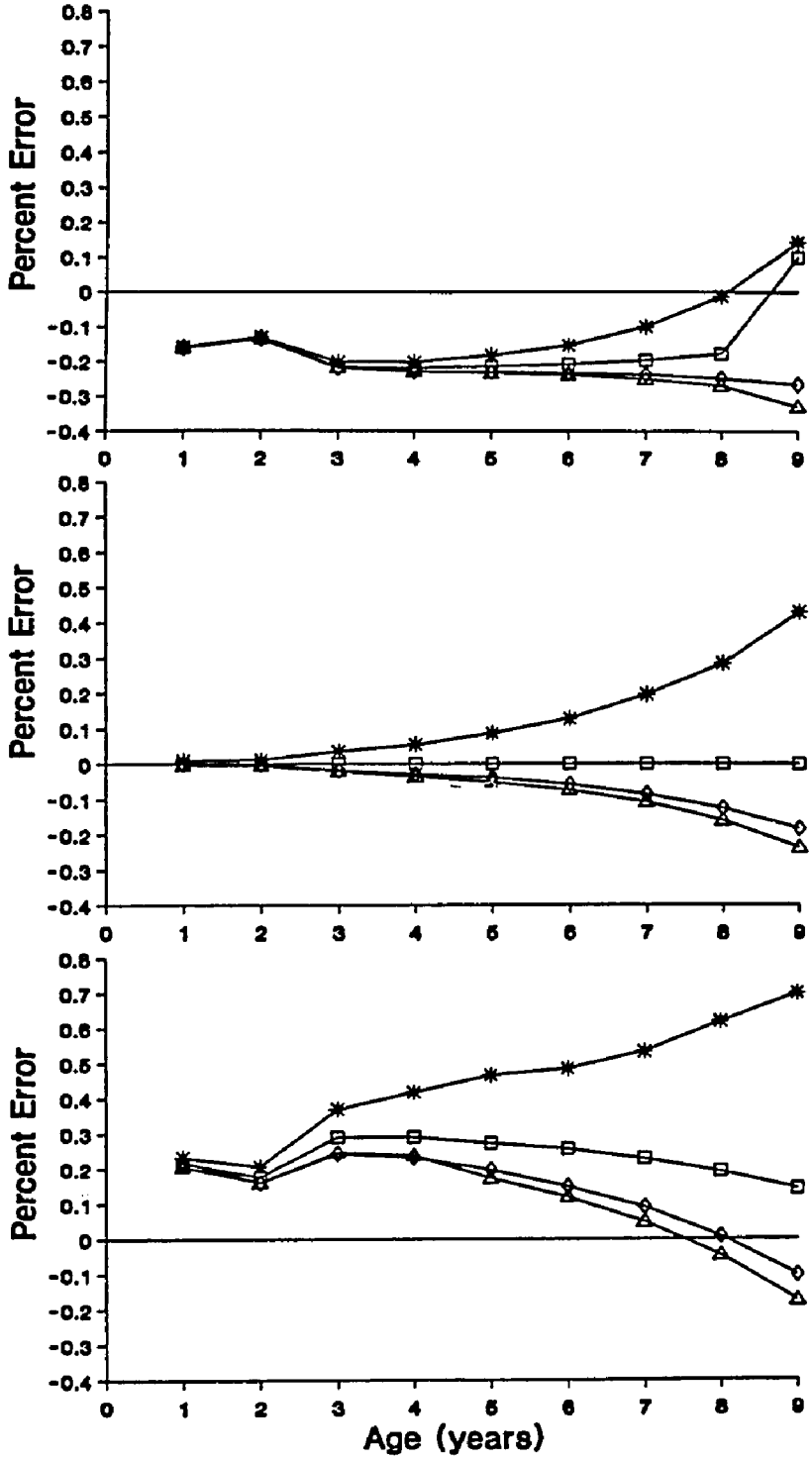

Figure 4.1. Percent error in the estimated population size from the virtual population analysis conducted on the simulated cohort. Twelve outcomes are shown from the analysis using four levels of terminal fishing mortality for each of the three different levels of natural mortality. Natural mortality set at M=0.2 (top), M=0.3 (middle), and M=0.4 (bottom). Levels of F_t are 0.2 (star), 0.4 (square), 0.7 (diamond), and 0.9 (triangle).

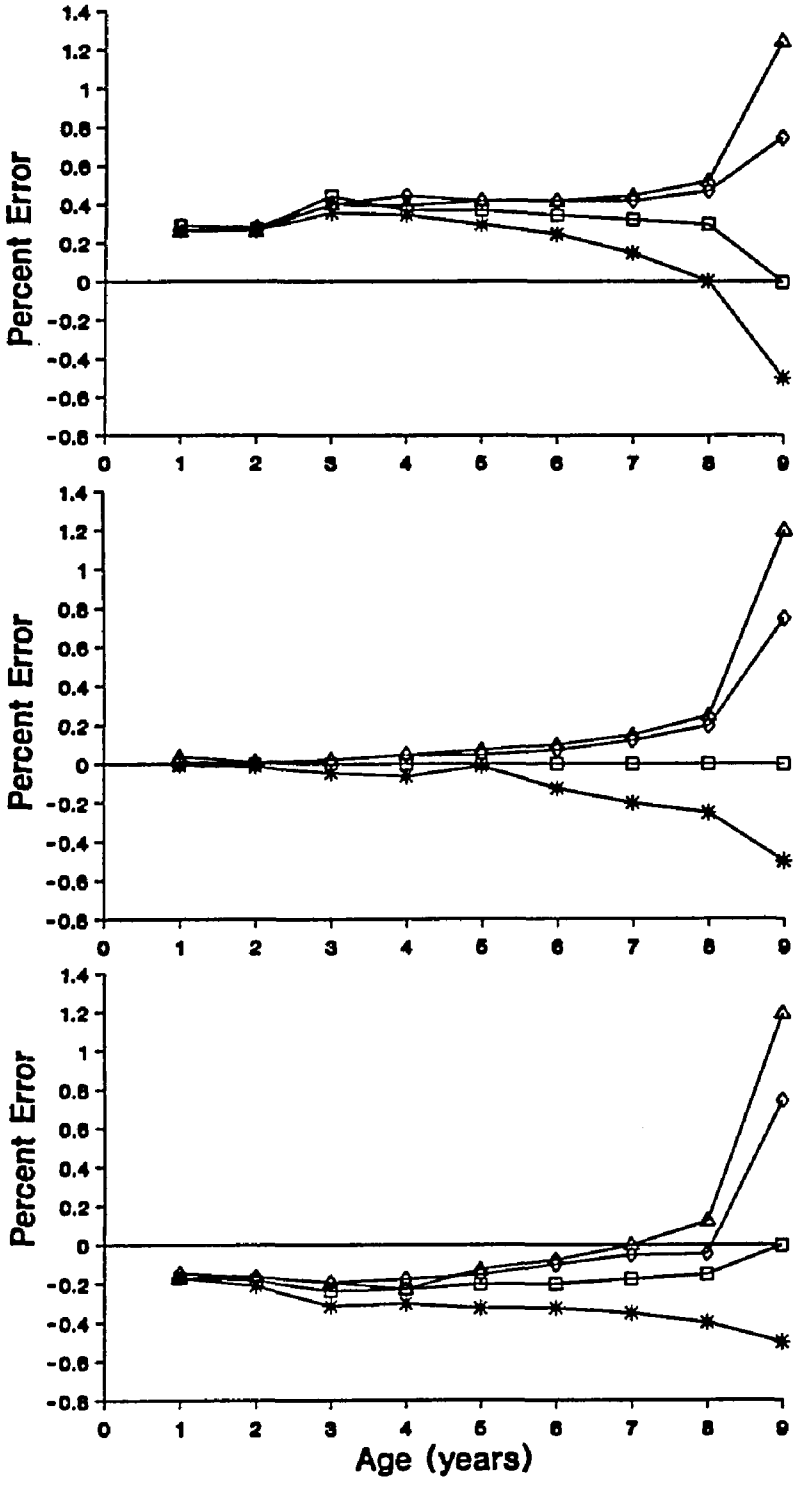

Figure 4.2. Percent error in the estimated F-vectors from the virtual population analysis conducted on the simulated cohort. Twelve outcomes are shown from the analysis using four levels of terminal fishing mortality for each of the three different levels of terminal fishing mortality. Natural mortality set at M=0.2 (top), M=0.3 (middle), and M=0.4 (bottom). Levels of F_t are 0.2 (star), 0.4 (square), 0.7 (diamond), and 0.9 (triangle).

Figure 4.1 shows that for M=0.4 and F_t=0.2, percent error in estimated population sizes less than age 4 is as great as 35% compared to a 25% error for F_t=0.9 at the same level of M. Furthermore, even if the correct value of F_t was chosen (0.4) the percent error propagated in the estimated population size is greater than 20% at ages 3 and 4 and no less than 15% at age 2 where most of the fishing on the hypothetical cohort occurs. The choice in F_t appears to affect the percent error in the estimated population size at age less than a wrong choice in natural mortality. An important point here is seen in figure 4.1 (M = 0.2) where a wrong choice in M by only a small fraction (0.1) leads to under-estimating the population size at age 3 by 20%, almost 1.5 million fish, for any given level of F_t. This could translate into significant error when assessing a fish population (i.e. setting quotas).

The estimated F-vector is also significantly affected by a wrong choice in M. Figure 4.2 indicates that under-estimating M over-estimates (positive bias) the F-vector for almost all age groups in the simulated cohort while over-estimates in M lead to under-estimates (negative bias) in the F-vector. Again the magnitude of the bias in either direction seems to depend on the initial choice in F_t as well as the natural mortality. For example, F at age 3 is under-estimated by 20-30% (depending on F_t) in the case where M = 0.4 in Figure 4.1. However, for M=0.2 at the same age in the simulated cohort higher levels for F_t can over-estimate F by as much as 40%. It is clear, however, that regardless of which level of F_t is chosen the estimated F-vectors converge adequately by age 3 in this simulated cohort. Jones (1981) using Pope's (1972) approximation to the cohort analysis first

identified the convergence property associated with various choices in terminal fishing mortality. These results using an iterative solution attempt to further quantify the direction and magnitude of potential biases in VPA estimates. The estimated F-vector and population size at age from this VPA solution appears to be more sensitive to a wrong choice in M than F_t.

In most assessments involving VPA, bias will be difficult to determine because natural mortality, terminal fishing mortality, and other input parameters are poorly known. Even so, it may be more important and practical to quantify the uncertainty in the model output which results from parameter input uncertainty. Figure 4.3 and 4.4 illustrate the model output uncertainty from the VPA applied to the simulated seatrout cohort (M=0.3 and F_t=0.4) in terms of SSBR and recruitment to age 2, respectively. Figure 4.3 shows the distribution of SSBR based on 3000 VPA outcomes from the Monte Carlo simulations, when M and F_t are randomly selected from both the uniform and triangular input probability distributions. It is evident that the distribution in SSBR, when the uniform input distribution is used, appears more positively skewed even though its range is similar to that of the triangular input distribution. For both, SSBR ranges from approximately 8% to 35%. Note also that the most likely value differs depending on the choice of the input distribution. Random selections of M and F_t from the uniform distribution result in a modal value of 10% SSBR while selections from the triangular give 17%. The computed deterministic estimate of SSBR for the simulated cohort was coincident with the modal value from the triangular input distribution at 17%. Although the

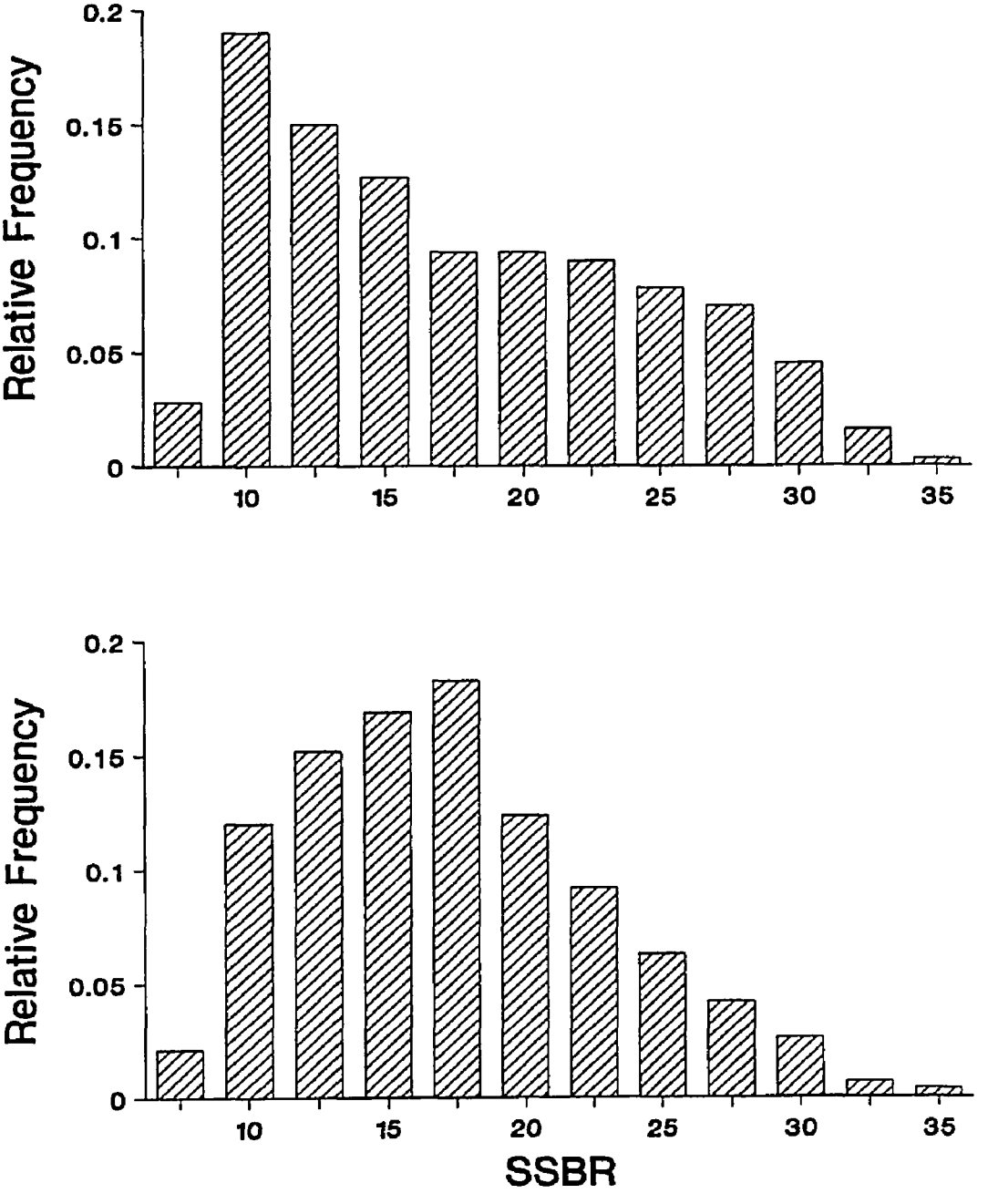

Figure 4.3. Distribution of spawning stock biomass per recruit (SSBR in percent) based on 3000 Monte Carlo simulation outcomes when natural mortality and terminal fishing mortality are randomly chosen from the uniform (top) and triangular (bottom) input distributions.

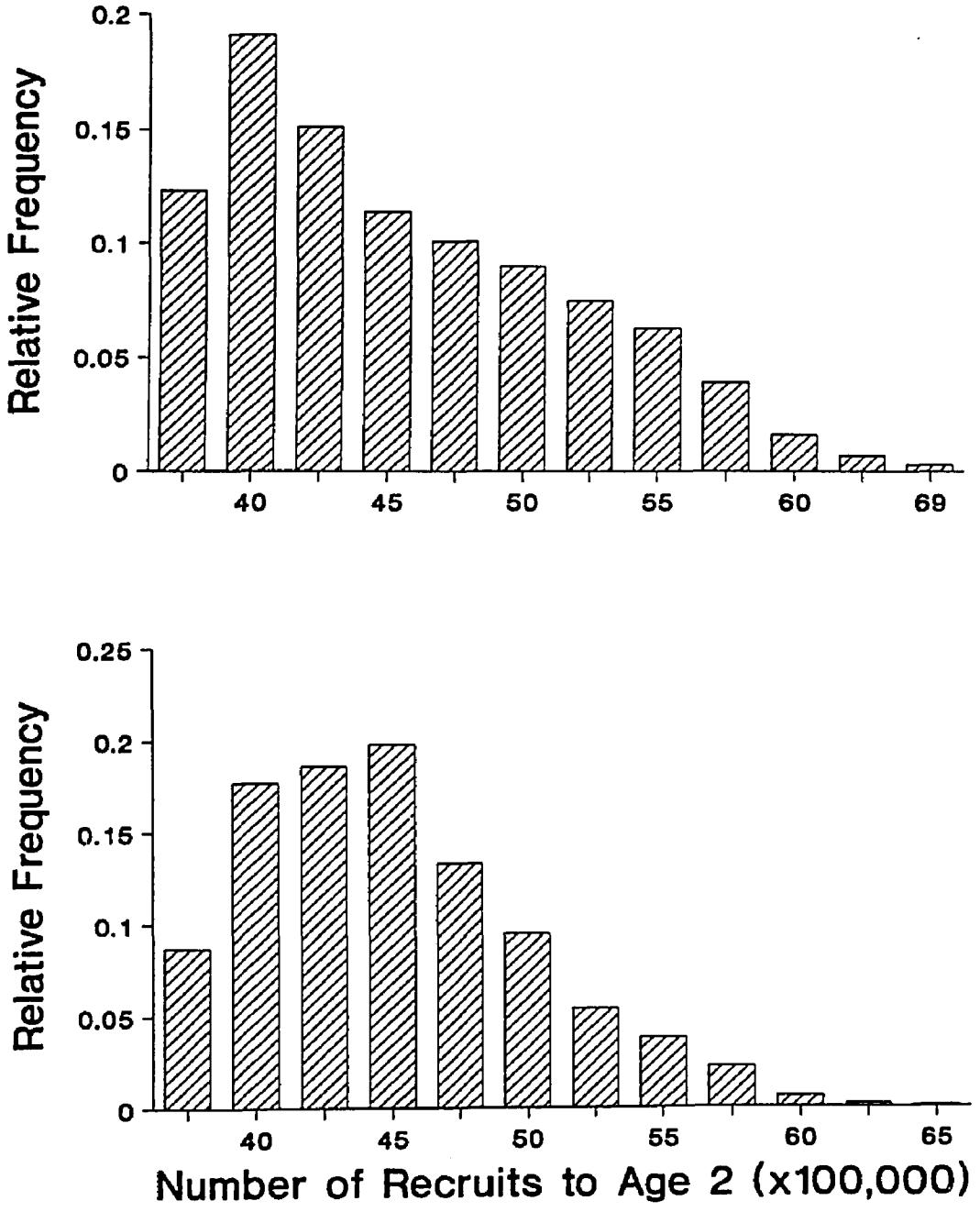

Figure 4.4. Distribution of numbers of recruits to age 2 based on 3000 Monte Carlo simulation outcomes when natural mortality and terminal fishing mortality are randomly chosen from the uniform (top) and triangular (bottom) input distributions.

distributions in SSBR are positively skewed, more than half (60-65%) of the simulated VPA outcomes fell below the deterministic estimate (17%). Restrepo and Fox (1988) have suggested that skewness associated with the output distribution of percent yield in their model is attributed to the non-linearity of the yield-per-recruit model. This may clearly be the case in Figure 4.3 where the skewness associated with the VPA output distribution of SSBR (Figure 4.3) is due to its non-linear solution, despite the fact that M and F_t were randomly selected from the uniform input distribution. Model output distributions may be more skewed (non-normal) when more complex VPA approaches are used or other sources of input parameter uncertainty, as well as covariance between input parameters, are incorporated into the VPA model. This could lead to misinterpreted conclusions about the spawning potential of the stock if one assumes that the deterministic VPA output of SSBR represents an expected value with an equal probability of being above or below this estimate.

The output distribution of the number of recruits to age 2 from the Monte Carlo simulations is shown in figure 4.4. Age 2 fish represent the size at which spotted seatrout become fully recruited to the fishery. The shape of these distributions appear similar to SSBR for their respective input distributions. Numbers of recruits to age 2 range from a low of 3.7 million to a high of 6.9 million fish. Random selections of M and F_t from the uniform input distribution result in 4.0 million fish at age 2 as the most likely value while selections form the triangular give 4.5 million fish, which is also the computed deterministic estimate for the simulated cohort.

The distributions for both output variables of SSBR and recruitment to age 2 appear to be best characterized as log-normal. Restrepo and Fox (1988), using the Monte Carlo approach to characterize uncertainty in Beverton's yield-per-recruit model, show that the output distribution in percent change in yield is also log-normally distributed. This may be a general case in models which utilize simple exponential equations as the basis for computation.

We compare the extreme parameter method to the Monte Carlo simulation approach in their ability to describe the model output uncertainty in Figure 4.5. Here, the extreme parameter method is simply an approach where one chooses combinations of the most likely (or some midpoint value) input parameter values and well as estimates at the lower and upper bounds. We chose the triangular input probability distribution for comparison because of the numerous coincident values for natural mortality reported in the literature. It is clear that the Monte Carlo approach (sample size can be set at any number) gives a much fuller picture in the VPA model output uncertainty (Figure 4.5), since only 9 combinations are possible with the extreme parameter method. Although the range in estimated SSBR values is roughly the same for both approaches the most likely value differs considerably between them, 10% vs. 17% for the Monte Carlo approach. Moreover, the advantage in characterizing the VPA model output, using the Monte Carlo simulation, is that one can ascertain the level of probability that the true value falls below the deterministic point estimate of SSBR.

In this study we wish to present an alternate approach to incorporating uncertainty into simple (overparameterized) VPA when

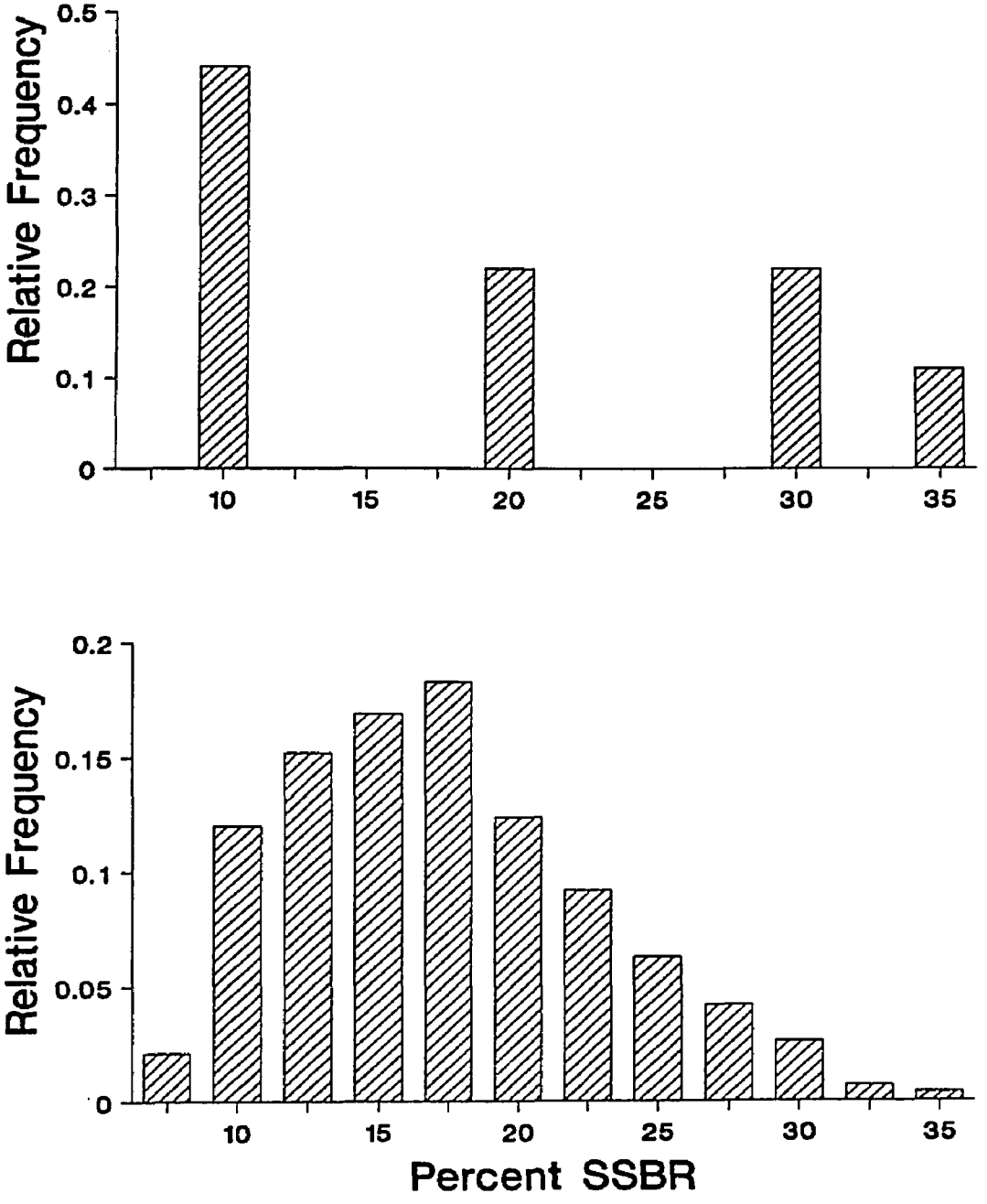

Figure 4.5. Comparison of the extreme parameter method (top; N=9) and the Monte Carlo based VPA simulation (bottom; N=3000) for distribution of spawning stock biomass per recruit (SSBR in percent).

auxiliary information for "tuning" is unavailable, such as for the fishery for spotted seatrout in Louisiana. Depending of the complexity of the VPA model used, error can be propagated from uncertainty in a host of input parameters (Saila et al. 1985), such as estimation of total catch; catch at age; weights at age; natural mortality rate; and terminal fishing mortality rate. Prager (1988) analyzes the sensitivities and variances of many of these input parameters utilizing numerical methods and an approximation similar to MacCall's (1986) for a VPA solution. Further error can arise from covariances between the individual input parameters themselves. However, here we focused on error in natural mortality and terminal fishing mortality rates as independent variances and their effect on an iterative solution to simple VPA output in terms of the spawning potential ratio using Monte Carlo simulation.

By incorporating the Monte Carlo method into other simple VPA assessments using estimated catch data for a specific fishery variance about point estimates of SSBR can be estimated. Figure 4.6 illustrates this point by applying the Monte Carlo based approach (using the triangular input distribution) to the estimated cohorts of spotted seatrout in Louisiana from 1980 through 1986. The variation about point estimates of the SSBR values for each cohort from the model output is given as the 5.0^{th} and 95.0^{th} percentiles of the distribution of outcomes. Due to the large number of Monte Carlo simulations (N=3000) for each cohort separately the observed distributions should provide a pretty good empirical approximation to the log-normal probability distribution. For all cohorts of spotted seatrout between 1980 and

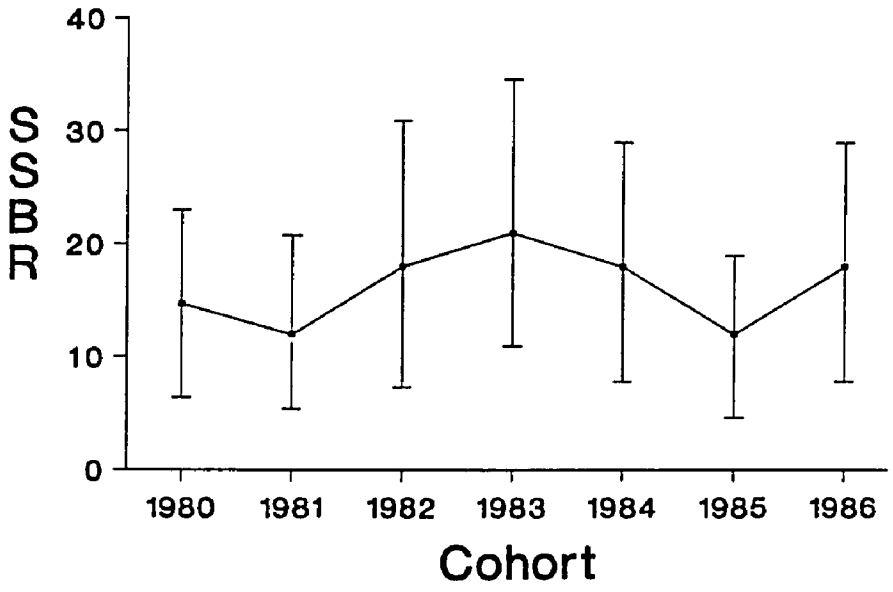

Figure 4.6. Variance (2 standard deviations) in spawning stock biomass per recruit (SSBR in percent) estimated from the Monte Carlo based VPA simulation and applied to the 1980 through 1986 cohorts of spotted seatrout.

1986, only the 1983 cohort appears to have reached a 20% level of the SSBR, considered to be a minimum safe level of female spawning biomass per recruit by many fishery scientists and managers. Moreover, the uncertainty in the input parameters translates into considerable variability about the point estimate. In this case, even though the point estimate of SSBR was 20% in 1983 the chance of being wrong and at some value below this threshold level was 60%. This point is demonstrated in Figure 4.3 where approximately 60% of outcomes in SSBR from the Monte Carlo simulations fell below the deterministic point estimate of 17%.

If the objective of management is to provide for a safe level of spawning stock biomass (measured in the SSBR) above some minimum threshold, then decisions concerning management regulations should also take into account the uncertainty associated with point estimates. Stated another way, if current regulations translate into a point estimate of SSBR sufficient only to meet the minimum safe level, then one should ask the question, what is the probability that the actual level of SSBR falls below this threshold. Prudent management of a valuable stock, such as spotted seatrout, would strive to minimize the chances of observing SSBR levels below a biologically rational threshold. Management of the stock should proceed on the basis of two important decisions: 1) the acceptable chance of being incorrect in the estimated level of SSBR and 2) the biologically rational threshold level of SSBR for the stock. If for instance the threshold level of 20% is chosen for the stock, then the fishery should be regulated such that the acceptable chance of being incorrect in the estimated SSBR (i.e. 30%) is

met. This could be achieved through the implementation of management strategies (i.e. minimum sizes, bag limits, quotas etc.) to reduce fishing mortality such that there is a shift in the estimated distribution into higher levels of SSBR, thereby meeting the threshold level requirement and minimizing the chance of being incorrect.

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February 21, 1992

Mr. T. E. Helser
Coastal Fisheries Institute
Center for Wetland Resources
Louisiana State University
Baton Rouge, Louisiana 70803-7503

Dear Mr. Helser:

We are pleased to grant permission for you to include the following article in its entirety in your doctoral dissertation and microfilm versions thereof, provided that the original source is clearly identified:

Helser, T. E., R. E. Condrey, and J. P. Geaghan. 1991. A new method of estimating gillnet selectivity, with an example for spotted seatrout, Cynocion nebulosus. Can. J. Fish. Aquat. Sci. 48: 487-492.

Sincerely,

David G. Cook
Editor
Canadian Journal of Fisheries and
Aquatic Sciences

Canada

VITA

Thomas Earl Helser, son of Robert Helser and Agnes Helser, was born February 25, 1960, in Appleton, Wisconsin. He attended Outagamie County Public Schools and graduated from Appleton High School West, in 1978. In September, 1978, Thomas entered undergraduate studies at the University of Wisconsin, Stevens Point, where he received the degree of Bachelor of Science in Biology in August, 1982. While at the University of Wisconsin, Thomas was actively engaged in plant physiology research in the electron microscopy laboratory and was awarded the Brian Eagen Research Scholarship by the Department of Biology. In September, 1982, he entered the United States Peace Corps and served as an aquaculture extension agent in the Nawal Parasi District of Nepal. After returning to the United States in 1983, Thomas was employed by the University of Florida as a Biological Scientist in both the Departments of Physiological Sciences and Urology. In September, 1985, he entered graduate studies in the Department of Allied Aquacultures and Fisheries at Auburn University and was awarded the degree of Master of Science in August, 1987. His Thesis, entitled Age and Growth of Spanish Mackerel in the Northern Gulf of Mexico With Implications for Recreational Fishery Management, was published and has served as a scientific working document for the management of the mackerel stocks by the Gulf States Marine Fisheries Commission. Thomas entered his doctoral program in the Department of Oceanography and Coastal Sciences at Louisiana State University in September, 1987. During his tenure as a graduate research assistant he received a joint appointment by the Gulf of Mexico and the

South Atlantic Fishery Management Councils to serve as a scientific member of the Mackerel Stock Assessment Panel. He has also served on a number of other fishery management advisory committees for the Louisiana Department of Wildlife and Fisheries. In 1990, Thomas was awarded the Theodore Ford Scholarship for his scientific work on the spotted seatrout stocks in coastal Louisiana.

DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Thomas E. Helser

Major Field: Department of Oceanography and Coastal Sciences

Title of Dissertation: Development of Various Quantitative and Analytical Methods for the Analysis of the Dynamics of Fish Populations: An Application to the Spotted Seatrout Population in Coastal Louisiana.

Approved:

Richard Condrey
Major Professor and Chairman

Daniel Fogel
Dean of the Graduate School

EXAMINING COMMITTEE:

James P. Geaghan

Ilona C. Wang

James Arnold

Charles Wilson

Date of Examination:

February 5, 1992